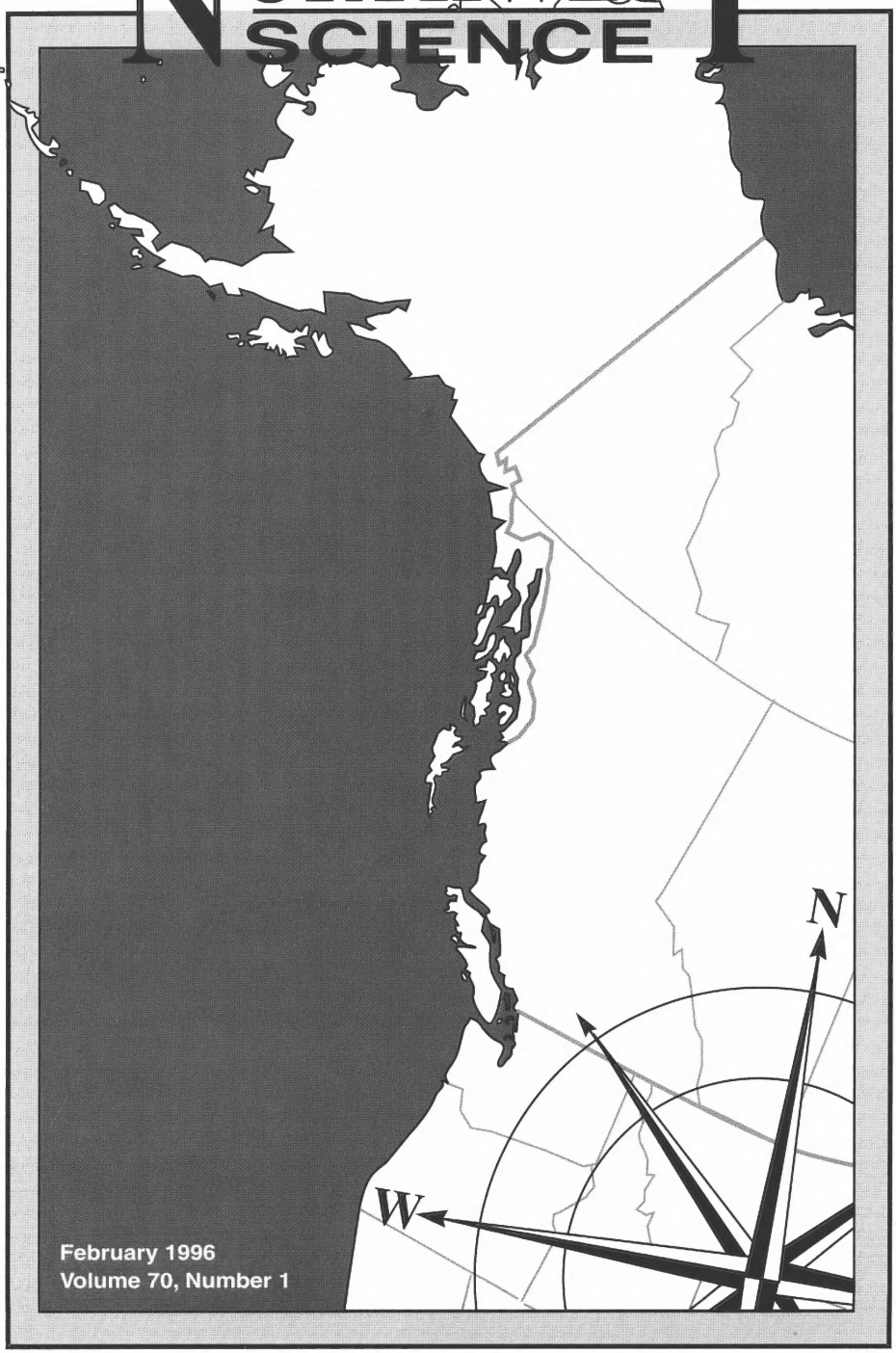
NORTHWEST SCIENCE



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Notice of Annual Meeting

The 69th annual meeting of the Northwest Scientific Association will be held jointly with the Wildlife Society and Lichen Guild on 20-23 March 1996, at Pacific Lutheran University in Tacoma, Washington. In addition to several contributed paper sessions, there will be symposia on climate change in the Pacific Northwest, geology of the Olympic Peninsula, and the Eastside Forest Assessment. There will be field trips focusing on various aspects of natural resources of the Olympic Peninsula, Nisqually Wildlife Refuge, and Puget Sound region. Both members and non-members of the Northwest Scientific Association are welcome at the meeting, and students are especially encouraged to attend.

Associate Editor Change

Dr. Steven Ghan (Battelle-Pacific Northwest Labs, Richland, Washington) recently accepted the position of Associate Editor for Mathematics and Computer Applications for *Northwest Science*. He received his Ph.D. in meteorology from MIT, and has authored many articles related to modeling clouds and aerosols in global atmospheric models. He is currently working on regional climate and hydrology issues in the Pacific Northwest. I appreciate Dr. Ghan's willingness to serve as Associate Editor and look foward to working with him.

—The Editor

Northwest Science Forum

Readers are reminded that *Northwest Science* is now accepting submissions for the Forum section of the journal. You are invited to submit short articles, opinion pieces, or letters with a focus on science and natural resource issues in the Pacific Northwest. This is an opportunity to share your views with colleagues in a less structured format. Forum authors are encouraged to address controversial issues and get out on the edge a bit. Submit articles directly or contact the Editor for more information.

—The Editor

In Memory

Two outstanding scientists, both Honorary Life Members of the Northwest Scientific Association, passed away during the past year. Dr. Rexford Daubenmire, plant ecologist at Washington State University, advanced our understanding of the terrestrial ecology of the Pacific Northwest and the biogeography of North America. Dr. Stanley Gessel, soil scientist at the University of Washington, was a pioneer in research on biogeochemical cycling in forest ecosystems and was a strong advocate of long-term soils studies. These distinguished scientists will be greatly missed by their students and colleagues.

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Habits of Bald Eagles Wintering along the Upper John Day River, Oregon

Abstract

We investigated the ecology of bald eagles (*Haliaeetus leucocephalus*) wintering along the upper John Day River in northeastern Oregon from late-November through March, 1991-92 and early-December through March, 1992-93. Our primary objective was to locate night roosts. Secondary objectives were to document eagle abundance, locate foraging areas, and describe food habits. The number of eagles peaked at 96 during early-February 1992 and 64 in early-March 1993. Midwinter Bald Eagle Counts and Christmas Bird Counts suggest that the number of bald eagles wintering in the area has increased recently. Primary foraging areas were the John Day River between Picture Gorge and Blue Mountain Hot Springs, the North Fork of the John Day River, and Fox Valley. Mammal carrion was an important food; fish, ground squirrels (*Spermophilus* spp.), and birds were also utilized. Sixty-one night roosts were located and 19 more were suspected. Eighty-five percent of roosts were used by ≤ 5 bald eagles. Only 16% of roosts identified in 1991-92 were used in 1992-93 because eagles moved frequently in response to small, scattered, and ephemeral food supplies. Sixty-six percent of the night roosts were in conifers, 33% were in black cottonwood (*Populus trichocarpa*), and one roost (2%) was in a mixed western juniper (*Juniperus occidentalis*), deciduous tree stand; 62% of roosts were on private land. Non-commercial and unregulated cutting of trees on private land is done to expand fields for agriculture, obtain firewood, or clear land for subdivision and other purposes, and commercial harvest of cottonwoods is becoming economical. Consequently, the potential for losing roosts is great, resulting in the possible degredation of wintering habitat for bald eagles. We conclude with management recommendations for monitoring the bald eagle population and managing their foraging and roosting habitats.

Introduction

Bald eagles are highly mobile, predatory birds that inhabit North America. They capture live prey, scavenge, and steal food from other predators. They eat a wide variety of food and can fly long distances in search of prey. Bald eagles migrate from areas where food is scarce during winter to areas where food is more available. Wintering areas with consistent food supplies develop a tradition of bald eagle use. The number of bald eagles that congregate at wintering areas and the duration of their stay is directly related to the abundance and availability of food. Many wintering areas have been identified (Spencer 1976), and the habits of wintering bald eagles have been intensively studied (Stalmaster 1987, McClelland et al. 1994).

Communal roosting has been defined as: > 1 eagle for at least 1 night (Buehler et al. 1991); and ≥ 3 eagles for ≥ 2 nights (Anderson et al. 1985). Communal night roosts have been recognized as important components of wintering habitats (Anthony et al. 1982), and the Pacific States Bald Eagle Recovery Team recommended that communal roosts be identified and protected (U.S. Fish and Wildl. Serv. 1986). In contrast, the importance of solitary roosting (1 eagle roosting alone) has received little attention (Buehler et al. 1991).

In Oregon, detailed studies of the habits of wintering bald eagles have been conducted in the Klamath Basin (Keister and Anthony 1983, Keister et al. 1985, Keister et al. 1987), Harney Basin (Isaacs and Anthony 1987), along the lower Columbia River (Watson et al. 1991, Garrett et al. 1993), in the Willamette Valley (DellaSala et al. 1989), along the Crooked River (Isaacs et al. 1993), and in northeastern Oregon (Isaacs et al. 1992). In all of these areas, abundant food attracted bald

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eagles that congregated at foraging areas and night roosts that were used consistently during and among winters.

Historical observations of bald eagles during late fall, winter, and early spring along the John Day River indicated that there were substantial numbers of bald eagles present from January through March and that communal roosts existed (M. Henjum, Oreg. Dep. of Fish and Wildl., pers. comm.). Consequently, there was concern about the potential impacts of habitat alteration and other human activities on the species, and a need to identify important winter habitats. The purpose of this study was to investigate the habits of bald eagles wintering along the upper John Day River. The primary objective was to locate night roosts. Secondary objectives were to document eagle abundance, identify foraging areas, and describe food habits.

Study Area

The study area included the John Day River and its major tributaries upstream from Service Creek. This included the John Day River, Camas Creek, the North, Middle, and South Forks of the John Day River, and Fox and Long Creek Valleys (Figure 1). Service Creek was chosen as the downstream limit to the study area because access was limited and because eagle use was thought to be less below that point. Elevations ranged from 500 m at Service Creek to 2755 m on Strawberry Mountain. Elevations of survey routes ranged from 500-1555 m (Table 1).

Vegetation and climate vary considerably over the study area because of the wide range in elevations. Major vegetational communities in order of increasing elevation are shrub-steppe, steppe, ponderosa pine (*Pinus ponderosa*), and white fir

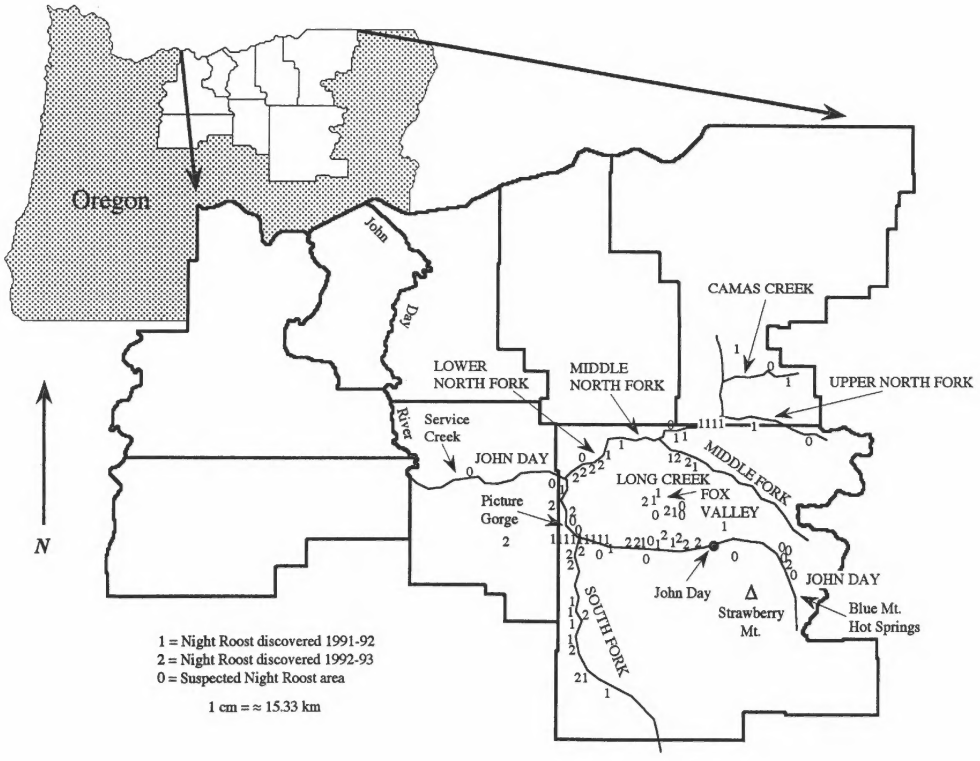

Figure 1. Survey areas and night roost locations for wintering bald eagles along the upper John Day River, Oregon, 1991-93.

TABLE 1. Bald eagle counts for the upper John Day River area, Oregon, 1991-93. Underlined numbers are peak counts for 1991-92, boxed numbers are peak counts for 1992-93. Route name is followed by the range of elevations on the route and approximate length of the route

Route	Count for the Week Beginning:																	Total	No. of	Eagles per	Eagles per
	Nov.	December			January				February				March								
Winter	30	7	14	21	28	4	11	18	25	1	8	15	22	29	7	14	21	Eagles	Surveys	Survey	km
John Day River above Picture Gorge; 686-1282 m; 116 km																					
1991-92	11	7	7	13	5	30	21	27	7	20	19	42	21	12	21	5	5	273	17	16	0.14
1992-93		9	9			21	31		20		10		22	11	10	14	8	165	11	15	0.13
John Day River below Picture Gorge; 500-686 m; 72 km																					
1991-92	7	3	7	5	16	9	13	10	8	6	6	5	8	2	3	2	4	114	17	7	0.09
1992-93		2	9		5	3	7		9		8		4	3	2	0	0	52	12	4	0.06
Camas Creek; 823-1341 m; 82 km																					
1991-92		7	9	3	9	4	2	2	6	7	6	6	3	1	4	2		71	15	5	0.06
1992-93		6	3		0	1	2		0		3		4		5	2	7	33	11	3	0.04
Upper North Fork; 695-975 m; 56 km																					
1991-92	5	4	4	11	8	11	8	14	10	16	26	6	4	2	2	0	0	131	17	8	0.14
1992-93		7	2			1	4		4		2		8		24	0	1	53	10	5	0.09
Middle North Fork; 632-695 m; 26 km																					
1991-92									6	5	12			1	0		0	24	6	4	0.15
Lower North Fork; 555-632 m; 32 km																					
1991-92	2	2	0	4	4	5	4	0	1	6	2	3	5	5	3	1	0	47	17	3	0.09
1992-93		8	3			8	9		5		5		2		1	2	1	44	10	4	0.14
Middle Fork; 739-1244 m; 89 km																					
1991-92	0	0	0	0	1	2	2	3	3	6	5	3	0	1	1	1	0	28	17	2	0.02
1992-93		1	1		4	6	0		0		0		3		1	0	0	16	11	1	0.02
South Fork; 719-1341 m; 89 km																					
1991-92	2	0	6	1	1	2	2	3	5	1	3	0	0	2	1	0	1	30	17	2	0.02
1992-93		2	1		1	3	2		0		9		14	5	5	3	3	48	12	4	0.04
Fox Valley; 875-1555 m; 68 km																					
1991-92				7		2	1	2	12	28	10	16	6	4	7	5	6	106	13	8	0.12
1992-93			1			4	2		3		3		1		16	26	22	78	9	9	0.13
Long Creek; 1085-1555 m; 50 km																					
1991-92						0	1	2	0	1	0	2	0	0	0	0	3	9	12	1	0.01
1992-93			0			0	0		2		0		0		0	4	3	9	9	1	0.02
Total Weekly Count																					
1991-92	27	23	33	44	44	65	54	63	58	96	89	83	47	30	42	16	19	833	17	49	0.07
1992-93		35	29			47	57		43		40		58		64	51	45	469	10	47	0.07

(*Abies grandis*) and Douglas-fir (*Pseudotsuga menziesii*) (Franklin and Dyrness 1973). Most of the floodplain of the John Day River and its major tributaries is privately owned and has been converted to pasture. Black cottonwood is common in riparian areas at lower elevations, especially along the John Day River between Picture Gorge and Blue Mountain Hot Springs. Mean annual precipitation ranges from 30-60 cm and a high proportion of the total annual precipitation falls as snow from October through March. January is the coldest month, with a mean minimum temperature range of -13 to -5 °C. July is the warmest month, with a mean maximum temperature range of 27 to 31 °C (Franklin and Dyrness 1973). The effects of elevation and aspect on temperature and precipitation are important natural factors influencing the distribution of vegetation types in the region.

Methods

Locating night roosts was our primary goal. In order to locate roosts, we had to become familiar with the diurnal habits of bald eagles on the study area. We used ground surveys by vehicle to count eagles, locate feeding areas, and document food habits. Counts and foraging observations were subject to the vagaries of weather (poor visibility, road closures), timing of surveys, and observer bias (experience, number of observers per survey), and were limited to two field seasons with different survey schedules (weekly in 1991-92 vs. once every two weeks in 1992-93). Eventhough the results of these observations are important to understanding our conclusions, their usefulness outside of the realm of this study may be limited.

Surveys were conducted from late-November through March, 1991-92 and early-Decem-

ber through March, 1992-93. Surveys usually began at ≈ 0900 h; after most eagles had left night roosts to feed. Age class (adult = all white head and tail, subadult = any degree of brown in head or tail feathers, or unknown = plumage not distinguishable), location, activity, and time were recorded for each eagle observed. We tried to complete surveys by 1400 h so that birds leaving feeding areas to soar, loaf, or return to roosts were not missed. Counts of bald eagles observed during surveys were totaled for survey weeks and used as an estimate of the minimum number of bald eagles on the study area. Foods utilized by foraging eagles and potential prey observed at foraging areas were recorded opportunely to describe diets.

Survey routes were driven in 4-wheel-drive vehicles weekly during 1991-92 and at least once every two weeks (except for late December) in 1992-93 (Table 1). We attempted to locate every bald eagle that was visible by naked eye, with binoculars, or with a 45X spotting scope. We drove at slow speeds (16-64 km / h) and stopped when necessary to scan the surrounding area. Driving routes were modified during the study to improve coverage and increase efficiency. Major changes were the addition of the Fox Valley and Long Creek routes based on reports of local residents and agency personnel, and eagle observations made during the first month of field work. During 1992-93 some routes could not be surveyed or were only partially surveyed due to weather-related road closures. Personnel from cooperating agencies helped with some counts.

Searches for roosts began by observing and mapping flights of eagles leaving feeding areas during late afternoon. Eagles were followed to night roosts by vehicle when possible, otherwise, if a consistent pattern of flights to an area was observed, that area was searched for a night roost. An area was determined to be a night roost when an eagle was present after dark. After a roost was located, tree species were recorded and the roost was mapped on a 1:24,000 U.S.Geological Survey topographic map. Subsequent counts of eagles using roosts were conducted as frequently as possible. Usually we searched for new roosts rather than monitor known roosts because of the large number of suspected roost areas. Eagles were counted leaving roosts at dawn or arriving at roosts at dusk. Time, age class, and flight direction were recorded for each bald eagle observed. Volunteers from local communities and personnel from cooperating agencies helped with counts at some roosts. In addition, general areas with suspected roosts were mapped based on observations of evening flights.

We defined solitary roosting as 1 eagle roosting alone and communal roosting as ≥ 2 eagles roosting together. Thus, a night roost could have solitary roosting one night and communal roosting another. We evaluated roost use by comparing the maximum eagle count at roosts to the percent of bald eagles using roosts with different maximum counts.

Monthly normal minimum temperatures and monthly normal precipitation at the town of John Day (Figure 1) for 1961-90 are from Owenby and Ezell (1992). Daily weather data measured at John Day (Natl. Climatic Data Cent., Asheville, N.C., unpubl. data) were used to calculate average daily minimum temperatures by month for 1991-93.

Results and Discussion

Timing and Abundance

Bald eagles were observed throughout both field seasons (Table 1, Figure 2). The highest count for 1991-92 was 96 during the week of 1 February (Table 1). High counts continued for the next 2 weeks in February, then decreased considerably from late February through March (Figure 2). In 1992-93, the peak count of 64 occurred during the week of 7 March (Figure 2). Counts for 1992-93 were lower than for 1991-92 during most of December, January, and February, but higher than the 1991-92 counts during March (Figure 2).

Our counts were the first to document eagle abundance on the entire study area. Historical counts for portions of the study area suggest that there has been a recent increase in the number of bald eagles that occur on the upper John Day River in winter. Midwinter bald eagle counts were conducted on portions of the study area from 1979-83 and 1988-1993. Midwinter counts for 1979-83 were 6, 8, 7, 1, and 1, respectively; 1988-93 counts were 10, 12, 12, 31, 25, and 34, respectively (Oregon Eagle Foundation, Inc., unpubl. data). Christmas Bird Counts conducted at John Day from 1981-92 included 0, 0, 3, 1, 1, 4, 4, 3, 3, 9, 3, and 9 bald eagles, respectively (T. Winters, pers. comm.).

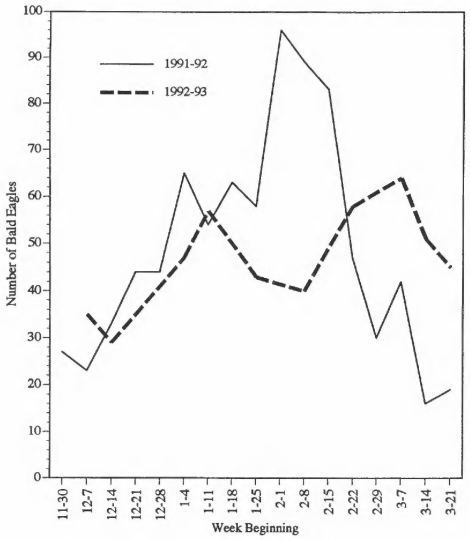

Figure 2. Weekly minimum estimates of bald eagles along the upper John Day River, Oregon, 1991-93.

Timing of peak eagle abundance in 1991-92 (early and mid-February; Figure 2) was similar to that observed in other wintering areas in eastern Oregon (Keister et al. 1987, Isaacs and Anthony 1987, Isaacs et al. 1992, Isaacs et al. 1993). Counts before February probably represented the over-wintering population whereas counts in February probably increased because of an influx of northward migrants from other wintering areas. The decrease in counts after the February peak was probably due to northward migration out of the area. Counts in 1992-93 (Figure 2) were similar to 1991-92 until early January. Counts then decreased until late February when they again began to increase to a second peak in early March. The decrease in the last half of January 1992-93 apparently was due to harsh weather and a lack of food. The late-January and early-February counts probably represented the over-wintering population. The increase in late February and early March was probably due to an influx of northward migrants from other wintering areas and the decrease in counts after the March peak was probably due to northward migration out of the area.

We speculate that the temporal differences in eagle abundance between years (Figure 2) was due to the effects of weather on the availability of prey. Winter 1991-92 was mild with average daily minimum temperatures greater than normal during all months and monthly precipitation less than normal during all months except November (Figure 3). That weather pattern resulted in little or no snow cover and rivers remaining ice-free throughout most of the study area all winter. In contrast, winter 1992-93 was much colder and had more precipitation than normal for most of the winter (Figure 3). That winter, deep snow and ice covered the landscape for extended periods except at the lowest elevations. Consequently, prey was probably more available during 1991-92 because of the mild weather, allowing eagles to stay on the study area rather than move to other wintering areas.

The relationship between elevation of survey route and timing of peak counts for individual

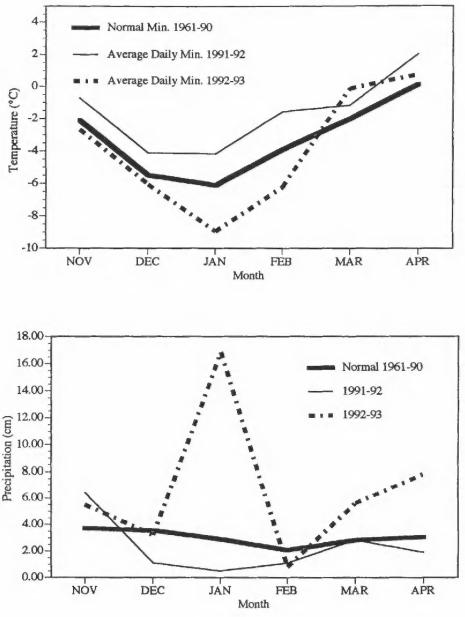

Figure 3. Average temperature and precipitation measured at John Day, Oregon. Monthly normal minimum temperatures and monthly normal precipitation from: Owenby, J.R. and D.S. Ezell. 1992. Monthly station normals of temperature, precipitation, and heating and cooling degree days, 1961-90, Oregon. Climatography of the U.S. No. 81. U.S. Dep. of Commerce, Natl. Climatic Data Cent., Ashville, N.C. 32pp.; daily weather data measured at John Day (Natl. Climatic Data Cent., Asheville, N.C., unpubl. data) were used to calculate average daily minimum temperatures by month for 1991-93.

routes also suggested that the effects of weather on prey availability affected the number of eagles on the study area. During 1991-92, the mild, dry weather resulted in similar foraging conditions throughout the study area. Consequently, peak counts on most routes occurred in early February (Table 1). In 1992-93, the cold, snowy weather resulted in thick ice and deep snow, especially at higher elevations. Consequently, peak counts on individual routes were spread over the winter, occurring later at higher elevations (Table 1) as food availability improved with the spring thaw.

Food Habits

Bald eagles were observed feeding (n = 41) on a variety of foods. Mammals were utilized most frequently (66%); fish (10%) and birds (2%) were also eaten; 22% of food items were not identified. Cow (*Bos taurus)* carrion was the most frequently observed food item and made up 37% of the mammalian food by number (n = 27). Other mammalian foods were mule deer carrion (*Odocoileus hemionus* ; 19%), ground squirrels (15%), jackrabbits (*Lepus* spp.; 7%), coyote carrion (*Canis latrans* ; 7%), cow placenta (7%), and unidentified mammals (7%).

Food habits of bald eagles are difficult to quantify for a variety of reasons (Mersmann et al. 1992). Since our observations were recorded opportunely, these data may not accurately quantify the food habits of bald eagles along the upper John Day River. We believe that large mammal carcasses, especially cows and road, hunter, and winter-killed mule deer and elk (*Cervus elaphus)* were important foods, but also think that fish, waterfowl, and ground squirrels were more important than the data suggest. The size of large mammal carcasses made them readily detectable whereas smaller prey was difficult to detect because of its small size and how quickly it could be consumed. Bald eagles consistently were observed along rivers with fish, near waterfowl concentrations, and were common near feed lots and calving areas for cattle. They were also observed consistently near fields with large populations of ground squirrels in late winter and early spring.

Night Roosts

We located 61 bald eagle night roosts, 37 in 1991-92 and 24 in 1992-93, and observed eagle activity that suggested night roosting in 18 other areas, 11 in 1991-92 and 7 in 1992-93 (Figure 1). In addition, 1 night roost reported in spring 1991 (prior to this study) was included as a suspected roost (P. Sweeney, U.S.D.A. Forest Serv., pers. comm.).

We recorded the results of 137 roost counts. Many more unsuccessful roost searches were conducted. Roost counts for a single night ranged from 0 to 21 bald eagles. The longest observed flight from a feeding area to a roost was 5.6 km. Although we believe that the major communal night roosts used by bald eagles were located, we suspect that other night roosts existed.

Night roosts were located on land managed by a variety of owners (n = 66): 62% were on private land, 26% were on land managed by Bureau of Land Management, 8% were on State of Oregon land, and 5% were on land managed by U.S. Forest Service. Night roosts (n = 61) were in conifers (66%), black cottonwood (33%), and a mixed western juniper, deciduous tree stand (2%). Fifty percent of conifer roosts (n = 40) were in ponderosa pine stands, 45% were in mixed conifer stands, 2.5% (1 roost) were in stands of western juniper, and 2.5% (1 roost) were dead conifers of undetermined species. Roosts were in mature and over-mature trees that were close to feeding areas and isolated from human activities. Our observations suggest that roost tree characteristics were similar to those reported for similar forest types in the Pacific Northwest (Anthony et al. 1982, Keister and Anthony 1983, Isaacs and Anthony 1987, Isaacs et al. 1993).

Only 6 of 37 (16%) night roosts and 2 of 11 (16%) suspected roost areas mapped in 1991-92 were observed being used in 1992-93. This degree of difference in roost use between years is unusual when compared to other wintering areas in eastern Oregon. Ten of 12 (83%) roosts discovered along the Crooked River in 1986 were reused in 1987 (Isaacs et al. 1987). Eleven of 14 (77%) and 15 of 24 (63%) roosts in northeastern Oregon were reused the following year, and 10 of 14 (71%) roosts were used 2 years after discovery (Isaacs et al. 1992). The reasons for this difference are unknown, but we suspect that the amount of suitable roosting habitat, and the amount and distribution of food were important. On most of the John Day River study area, suitable roosting habitat was abundant and evenly distributed whereas foraging opportunities usually were scattered and ephemeral. In contrast, suitable roosting

habitat was more localized and foraging opportunities usually were more consistent along the Crooked River and in other areas of northeastern Oregon, (F.B. Isaacs, pers. observation). Consequently, eagles along the John Day River likely changed foraging areas and night roosts more often than eagles in the other areas.

Classifying night roosts as communal may be appropriate only when a roost is monitored intensively for many nights throughout each of several winters. For example, a night roost was visible from our field station. We counted eagles roosting there as often as possible from 4 January to 24 March 1993. Eagles were present on 27 of 47 (57%) nights and ≥ 2 eagles roosted together on 22 nights (47%). During January there was at least 1 bird present each night counted (n = 11). In February, 1 or more eagles were present on 76% of the nights observed (n = 21); in March no eagles were observed during 15 nights of observation. Although as many as 10 bald eagles used this roost on a single night, ≥ 2 eagles roosted together on 22 nights, and our counts averaged 2.0 eagles / night over the entire period, periodic counts might not have resulted in observation of ≥ 2 eagles on a given night. For instance, counts conducted on 5 January, 3 February, and 2 March would have documented use by just 1 bald eagle for one night.

Eighty-five percent (n = 61) of night roosts were used by ≤ 5 bald eagles and solitary roosting was observed during 43 of 137 roost counts (31%). In addition, the highest count at 33% (n = 61) of night roosts was 1 eagle (Figure 4). Communal night roosting (≥ 2 eagles roosting together) occurred at 41 of 61 night roosts (67%). If we had used Anderson et al.'s (1985) definition of communal night roosting (≥ 3 eagles for ≥ 2 nights) only 5 roosts (8%) would have been classified as communal. We believe that many more night roosts would have been classified as communal if they had been monitored more often, especially if counts were made on successive nights immediately after discovery. We also believe that roosts used by small numbers of eagles were important. Fifty-four percent (n = 215) of bald eagles roosted in groups of 5 or less; 24.2 % roosted alone or with 1 other eagle (Figure 4). Consequently, a large percentage of this bald eagle population may depend on roost sites that would not be classified as communal roosts and may not be protected under existing definitions and regulations.

Human Activities

Although human activities were not quantified during this study, they deserve comment because of the potential for affecting wintering bald eagles. Potential conflicts between human activities and

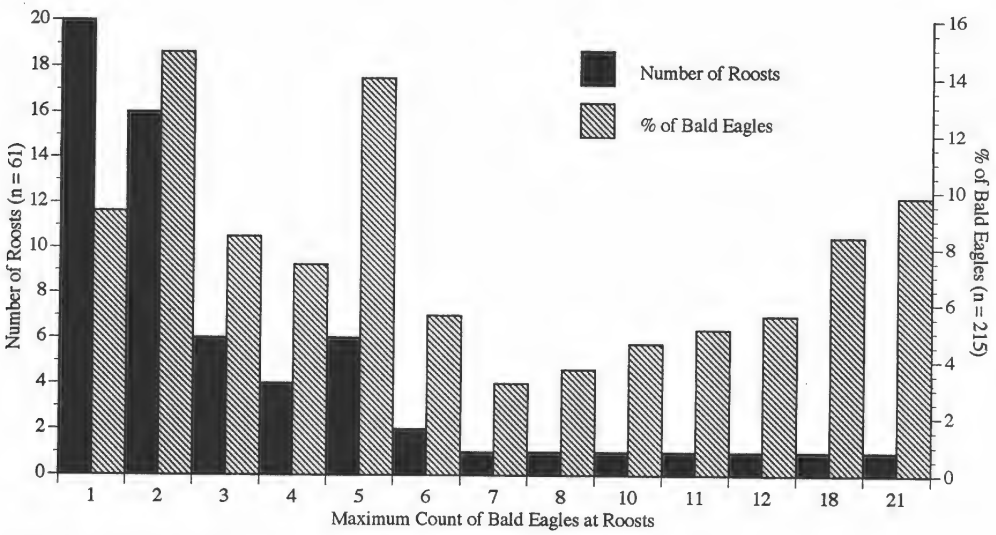

Figure 4. Use of bald eagle roosts located in the upper John Day River area, Oregon, 1991-93.

habitat use by bald eagles included agricultural and recreational activities at foraging areas, harvest of day perching and night roost trees, and ground squirrel control in foraging areas. Cutting of perch and roost trees for harvest or land clearing for agriculture were probably the greatest threats. A recent increase in the value of wood products has made it economical to harvest relatively small stands of cottonwoods and truck them long distances for processing. This jeopardizes eagle perching and roosting sites on the John Day River because 28% of roosts (n = 61) were in cottonwoods on private land.

Management Recommendations

Our results provide baseline data on bald eagles wintering along the upper John Day River. Future population monitoring efforts should be focused on primary foraging areas and night roosts. Foraging areas and roosts should be managed to maintain conditions that attracted eagles. Specific management recommendations follow:

Monitoring

- Continue conducting annual Midwinter Bald Eagle Counts and Christmas Bird Counts to document long-term trends in abundance and distribution of bald eagles wintering in the upper John Day River area. These counts cover two of the three primary foraging areas.
- Survey Fox Valley, the third primary foraging area, in February, March, or April, depending on the severity of the winter (later in years with more severe winters) because of its importance as a late-winter, early-spring foraging area, in order to document long-term trends in that area.
- Monitor roosts to determine roost boundaries and document use within and among winters. Monitoring over successive nights throughout successive winters might be needed to understand use patterns.

Foraging Areas

- Maintain individual trees and stands of mature and overmature cottonwoods and conifers along river corridors to provide foraging perches. Large trees should be distributed so that they provide unobstructed views of foraging areas and are isolated from human activities.
- Maintain fish populations at or above current levels.
- Use non-poisonous rodent control measures to prevent secondary poisoning of bald eagles feeding on carcasses.
- Move large mammal carcasses away from roads to areas isolated from human activities to enhance foraging opportunities for eagles (Isaacs et al. 1993) and to reduce the chances of collisions with vehicles.

Roosts

- Document new roosts by describing roost trees, mapping locations, determining landowners, and documenting eagle use.
- Protect roosts from cutting and development by exempting roosts and a 400-m perimeter (Isaacs et al. 1993) from inappropriate tree cutting (cutting that doesn't improve roosting habitat) and construction.
- Avoid human activities within 400 m of roost boundaries from October through April.
- Maintain stands containing mature and overmature trees along river corridors, especially at or near documented roost locations. Restrict grazing in roosts if it is suppressing tree regeneration.
- Prepare site-specific management plans (U.S. Fish and Wildl. Serv. 1986) for roosts that are threatened with logging or development.

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Winter Foraging Response of Elk to Spotted Knapweed Removal

Abstract

Picloram was used to convert 110 ha of an historically cultivated grassland (hereafter old-field) from spotted knapweed (*Centaurea maculosa*) to grass on an elk (*Cervus elaphus*) winter range in western Montana. About 30 ha were left untreated. I hypothesized that knapweed removal would not: (H_0I) affect winter foraging activity of elk; (H_0II) affect winter diets; (H_0III) vary in its effects on foraging activity and diets across the first four winters after knapweed removal; and (H_0IV) affect elk population distribution. Elk walked in adjacent knapweed and grass stands indiscriminately, but foraged almost exclusively in the grass stand (H_aI). Diets sampled before and after knapweed removal were not rank correlated, and forages characteristic of the old-field (i.e., *Poa, Bromus, Phleum*) ranked higher in diets after knapweed removal (H_aII). Elk foraging activity was significantly higher in the first winter than in subsequent winters (H_aIII). A higher proportion of the estimated elk population used the old-field after knapweed removal (H_aIV). I concluded that abundant green grass attracted elk to the old-field in the first winter after knapweed removal. Cured grass apparently attracted elk foraging activity and affected winter diets to a lesser extent in subsequent winters. When planning knapweed removal, elk managers should consider preexisting range condition and knapweed density, occurrence of preferred forage species, current and desired elk distribution, and the probability of adequate rainfall for substantial grass growth in the first growing season after herbicide application.

Introduction

Knapweeds (*Centaurea* spp.) are Eurasian species occurring on over five million hectares in the northwest United States and southwest Canada (Lacey 1989). Annual production of spotted knapweed (*C. maculosa*) may exceed 1,000 kg/ha on disturbed rangelands near roadside seed sources (Carpenter 1986). Tyser and Key (1988) also reported the invasion of spotted knapweed (hereafter knapweed) into relatively pristine fescue grasslands with a coincident decline in native plant diversity.

Winter ranges of Rocky Mountain elk (*Cervus elaphus nelsoni*) typically include rangelands (Lyon and Ward 1982) vulnerable to knapweed invasion (Mooers 1986). Elk are not obligate grazers, as evidenced by the 151 winter forages listed by Nelson and Leege (1982), but may lose foraging efficiency (Wickstrom et al. 1984) where knapweed dominates productive grasslands. Although speculative, an unpublished Forest Service report (Spoon et al. 1983) has often been referenced to justify warnings of future elk declines as knapweed spreads (Lolo National Forest 1991). Bedunah and Carpenter (1989) extrapolated the results of herbicide trials to imply a potential 2.4-fold increase in range carrying capacity for elk following knapweed control and concurrent grass production gains. However, results reported by Lavelle (1986) suggest elk can incorporate knapweed into their winter diets. Participants at the 1989 Knapweed Symposium identified knapweed impacts on elk winter ranges as a research need (Fay and Lacey 1989).

In May 1989, knapweed was removed from most of an historically cultivated grassland (hereafter old-field) on an elk winter range in western Montana. This vegetation conversion provided an unusual opportunity to study elk dietary responses because the vegetation composition of the old-field was unique in comparison with surrounding habitats; thus, dietary changes caused by old-field treatments presumably would be indicated by corresponding changes in proportions of old-field grasses in elk feces. I hypothesized that knapweed removal would not: (H_0I) affect winter foraging activity of elk; (H_0II) affect winter diets; (H_0III) vary in its effects on foraging activity and diets across the first four winters after knapweed removal; and (H_0IV) affect elk population distribution.

Study Area

The study focused on a 140-ha old-field in the northwest portion of the Threemile Wildlife Management Area (TWMA), located in Ravalli County, Montana (Figure 1). The old-field is 1,340-1,460 m above sea level on the west slope of the Sapphire Mountains and normally receives 32 cm of

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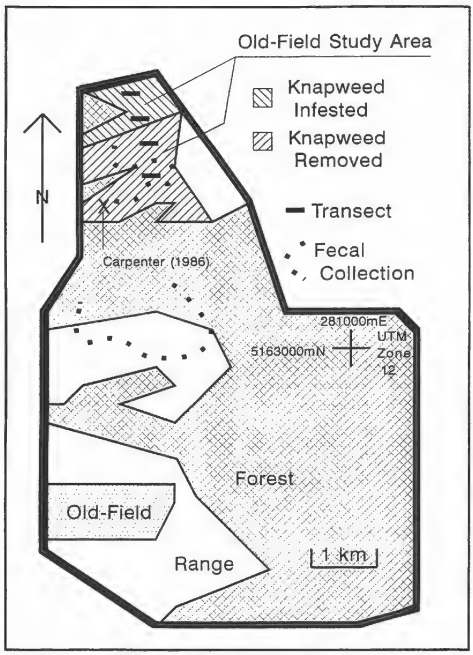

Figure 1. Juxtaposition of study sites and vegetation zones within the winter home range (adapted from Beall [1974:70], heavy outline on figure) of the Threemile elk population, 1990-1993.

annual precipitation (Carpenter 1986). It is part of an ecotone between ponderosa pine (*Pinus ponderosa*) forest and native rangeland dominated by bluebunch wheatgrass (*Agropyron spicatum*), Idaho fescue (*Festuca idahoensis*), needlegrass (*Stipa* spp.) and arrowleaf balsamroot (*Balsamorhiza sagittata*). Livestock had been excluded since 1967, when the Montana Department of Fish, Wildlife and Parks (MDFWP) purchased the TWMA to maintain and enhance elk winter range.

Knapweed dominated the old-field by 1973 (Hakim 1975). Carpenter (1986) and Bedunah and Carpenter (1989) conducted herbicide trials on 2 ha of the old-field in 1985-1988 (Figure 1). On their control plots, annual production averaged 1,234.6 kg/ha knapweed and 711.7 kg/ha grasses, compared with 8.0 kg/ha knapweed and 1,582.9 kg/ha grasses on picloram-treated plots (Carpenter 1986). Prairie junegrass (*Koeleria macrantha*) and Kentucky bluegrass (*Poa pratensis*) increased significantly after treatment. Other grasses in the old-field included cheatgrass (*Bromus tectorum*), western wheatgrass (*A. smithii*), timothy (*Phleum pratense*), Idaho fescue, bulbous bluegrass (*Poa bulbosa*), and Canada bluegrass (*P. compressa*). Forbs and woody species were uncommon in the old-field.

On 5 May 1989, picloram was aerially broadcast (200 cc/ha) over about 110 ha of the old-field. About 30 ha were left untreated (Figure 1). D. J. Bedunah (pers. comm.) agreed the vegetation response to picloram visually resembled that measured during the earlier herbicide trials by Carpenter (1986) and Bedunah and Carpenter (1989). An abrupt demarcation between the grass (picloram-treated) and knapweed (untreated) stands was conspicuous from September 1989 through 1993. Grass growth in the old-field after knapweed removal began late in the 1989 growing season, and was likely stimulated by above-normal July-August rainfall. Grasses remained green through the first winter, but grass phenology returned to normal in subsequent growing seasons. Temperatures and precipitation were broadly similar across the four winters of study. The old-field generally was snow-covered in December-February and snow-free in March.

Methods

Unless otherwise stated, 1990 denotes December 1989-February 1990 (the first winter of study); likewise, 1993 denotes December 1992-February 1993 (the fourth and final winter of study).

H_0I: Foraging Activity

I counted track-trails (not individual tracks) and feeding craters in the snow as evidence of elk foraging activity in the old-field knapweed and grass stands during 1990-1993. Four parallel belt transects (2 x 80 m) were established for counting tracks and craters on each side of the demarcation between the knapweed and grass stands (Figure 1). Transects were either 50 or 400 m (approximately) from the demarcation. Sampling frequency depended upon enough snow to cover grass foliage and previously counted track-trails (hereafter tracks). Mean track and crater counts in the knapweed and grass stands were tested for differences using a paired t-test.

H_0II: Diets

Composite winter diets of elk were estimated by fecal analysis (Stewart 1967, Table 1). Fecal pellets

TABLE 1. Fecal-sampling design for estimating five winter diets of elk on the Threemile Wildlife Management Area. Each diet represented a corresponding composited sample of 1-2 pellets from each of N individual pellet-groups.

	Elk Pellet-Groups		
Diet	N	Location	Representation
GRAS90	250	Old-field	First winter after knapweeed removal (pellets collected on 25 February 1990); diet potentially affected by knapweed removal
GRAS91	80	Old-field	Second winter after knapweed removal (pellets collected on 3 February 1991); diet potentially affected by knapweed removal
GRAS93	250	Old-field	Fourth winter after knapweed removal (pellets collected on 22 March 1993); diet potentially affected by knapweed removal
KNAP90	82	1-3 km south of old-field	First winter after knapweed removal (pellets collected on 25 February 1990); diet potentially unaffected by knapweed removal
KNAP86	38	Old-field and immediate vicinity	Four winters before knapweed removal (data from Lavelle [1986], pellets collected December 1985-March 1986)

deposited during the current winter period were identified by color and shape (Eberhardt and Van Etten 1956). I was unlikely to mistakenly collect summer and fall depositions because most elk migrated to the study area in late November. Early-spring biases were avoided by selecting against freshly deposited pellets during late-winter collections. Composite samples included 1-2 pellets from many pellet-groups to incorporate a representative range of animal and temporal variation (Table 1). Microhistological analyses were performed by the Wildlife Habitat Laboratory at Washington State University, Pullman.

Diets of elk in the old-field were compared among four winters (Table 1); i.e., one (GRAS90), two (GRAS91) and four (GRAS93) winters after picloram treatment, and four winters before treatment (KNAP86). I sampled a fifth diet (KNAP90) to test for temporal-enhanced variation between the KNAP86 and GRAS90 diets. My sampling objective for the KNAP90 diet was to represent the same combination of foraging habitats which yielded the KNAP86 diet. Accordingly, I sampled the KNAP90 and all other diets within the winter home range of the Threemile elk population (as delineated by Beall [1974]). By subjective assessment of track patterns, I concluded that the influence of the picloram-treated old-field could be excluded from the KNAP90 sample by collecting pellets 1-3 km south of the old-field (Table 1, Figure 1). If elk foraging distributions represented by the KNAP90 and GRAS90 samples overlapped in the old-field, the probability of detecting actual elk dietary responses to knapweed removal was reduced.

Diets were compared by first calculating a mean winter diet composition from the five individual diets. The fewest forage taxa with mean percent compositions totalling $\geq 75\%$ were selected for further analysis. These principal forages were ranked by their percentages in each individual diet, and the five diets were compared using Spearman's rank correlation. Spearman's coefficients were segregated into three diet groups (i.e., KNAP versus KNAP, GRAS versus GRAS, KNAP versus GRAS; Table 1) and grouped coefficients were averaged as an index of diet similarity for comparison among groups. Principal forages were sorted by their occurrence in three habitat categories (i.e., old-field, surrounding native habitats, mixed) and rankings were compared.

H_0III: Temporal Trends

Snow depth was measured to the nearest 1 cm in the old-field whenever tracks were counted. Counts of tracks and feeding craters were tested for differences between years using a 1-way analysis of variance. Differences between years were interpreted, in part, by testing track and crater counts (dependent variables) for correlation with snow depth and julian day (independent variables), and multiple linear regression analyses were performed.

Julian day (beginning from 1 December) was presumed to reflect a gradual reduction in the ecological metabolism (Moen 1978) of elk between late-fall and mid-winter, cumulative forage removal, and deteriorating snow conditions (i.e., settling and crusting). Dietary differences between years were examined by comparing Spearman's rank correlation coefficients.

H_0IV: Elk Distribution

I estimated levels of winter elk use on the old-field for comparison with previous estimates by Beall (1974), Hakim (1975) and Lavelle (1986). I recorded all incidental observations of elk in the old-field vicinity. Group size was estimated whenever a group of elk left fresh and individually distinguishable track-sets headed in the same direction. Pellet-groups were counted on the transects in February 1990, and the total was expressed in pellet-groups/ha. A subjective assessment of low, moderate or high elk use was made following the descriptions of Beall (1974), considering all indications of elk presence. Annual aerial surveys of the Threemile elk population (single counts during March or April) continued through this study (J. E. Firebaugh pers. comm.). Differences in mean population size were tested with a t-test. The 1992 flight produced an outlying low count (13) that was omitted.

Results

Eighteen surveys of elk tracks and feeding craters were accomplished during the first four winters after knapweed removal (Figure 2). A lack of fresh snow prevented more than one survey in 1992. Corresponding fecal samples for diet estimation were not collected that winter.

H_0I: Foraging Activity

I counted 1,803 tracks and 190 feeding craters. Elk walked through adjacent knapweed and grass stands indiscriminately, but pawed only four (2.1%) of the craters in the knapweed stand (Figure 3). Therefore, I rejected H_0I and concluded that factors associated with knapweed removal attracted elk foraging activity (H_aI).

H_0II: Diets

Forty-eight forage taxa were identified from a combined 700 elk pellet-groups sampled by Lavelle

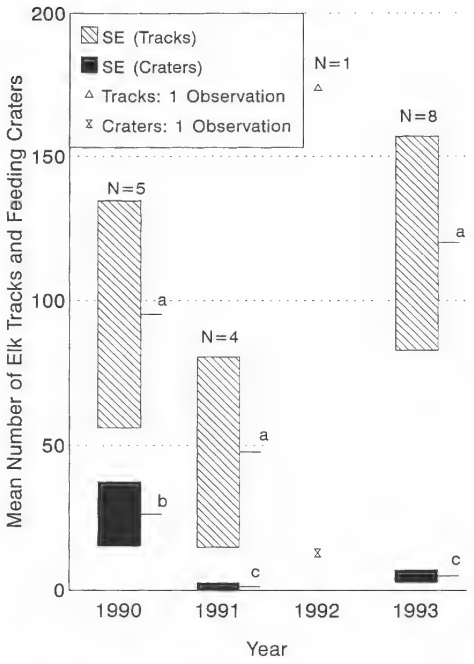

Figure 2. Mean counts (all transects combined) of elk tracks and feeding craters in an old-field on the Threemile Wildlife Management Area. ANOVA (1-way) on tracks by year: $F = 0.809$, $P = 0.47$; ANOVA (1-way) on craters by year: $F = 4.725$, $P = 0.03$. Different letters within groups (i.e., tracks or craters) denote significant differences ($P < 0.10$) indicated by Bonferroni test. N = number of surveys.

(1986) and the present study. Thirteen (27.1%) genera comprised >75% of the average winter diet (Table 2). KNAP and GRAS diets (Table 1) generally displayed more similarity within groups than between groups (Table 3). Spearman's coefficients indicated zero correlation between either KNAP diet and the GRAS93 diet, while the GRAS93 and GRAS91 diets displayed the highest correlation (Table 3). Genera characteristic of the old-field (i.e., *Poa, Bromus, Phleum*) ranked higher in GRAS diets than KNAP diets, while the rankings of widely distributed genera were variable (Table 2). Therefore, I rejected H_0II and concluded that factors associated with knapweed removal caused measurable shifts in elk winter diets (H_aII).

H_0III: Temporal Trends

Elk presence in the old-field (i.e., tracks) was consistent through four winters following

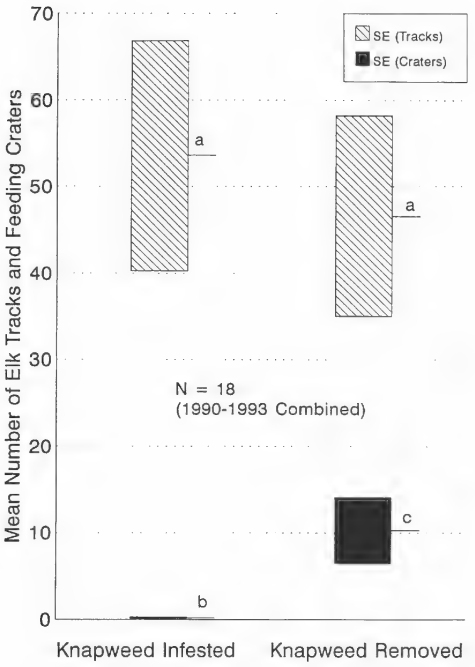

Figure 3. Mean counts of elk tracks and feeding craters by sampling site in an old-field on the Threemile Wildlife Management Area. Different letters within groups (i.e., tracks or craters) denote significant differences ($P < 0.05$). Paired $t = 0.54$ (tracks) and 2.65 (craters).

knapweed removal (Figure 2). Foraging activity indicated by craters was highest in 1990, and was significantly lower in subsequent winters. During 1990, tracks and craters were not correlated with snow depth, but tracks tended to increase as winter progressed (Table 4). During subsequent years, track counts declined as snow depths increased and winters progressed. The interaction of snow depth and julian day explained 41% of the variation in track counts during 1991-1993. The addition of data from 1990 reduced this explained variation to 8% (Table 4). The GRAS91 and GRAS93 diets displayed more similarity than any other diet comparison, and both diets were relatively dissimilar to GRAS90 (Table 3). Therefore, I rejected H_0III and concluded that elk responses to factors associated with knapweed removal persisted through the first four winters after knapweed removal, but were more pronounced in the first winter (H_aIII).

H_0IV: Elk Distribution

On 31 December 1989, I counted 95 fresh track sets heading west and verified that exactly 95 fresh track sets returned across the old-field. This indicated nearly four times the number of elk encountered during previous studies in the old-field (Table 5). Other measures of elk-use indicated a 170-1,200% increase in this study compared with previous reports (Table 5).

TABLE 2. Principal plant genera in five estimated winter diets of elk on the Threemile Wildlife Management Area (e.g., the KNAP86 diet [Lavelle 1986] pertains to the 1986 winter; Table 1).

	Diet Composition						
	Combined%		Rank By Winter				
Habitat Genus	$\bar{x}$	SD	KNAP86	KNAP90	GRAS90	GRAS91	GRAS93
Old-field grassland primarily							
Poa	12.20	6.49	7	2	1	1	1
Bromus	5.71	3.84	23	12	4	2	4
Phleum	2.58	1.99	23	18	9	10	14
Surrounding rangeland/forest primarily							
Berberis	7.13	4.10	2	5	6	8	9
Carex	6.55	4.53	5	1	3	15	16
Stipa	4.33	3.29	16	13	10	9	3
Artemisia	4.21	3.15	13	4	17	4	12
Balsamorhiza	3.70	1.59	14	7	12	6	10
Pseudotsuga	3.36	3.92	4	22	22	12	11
Calamagrostis	2.89	1.95	23	10	8	22	8
Both old-field and surrounding rangeland/forest							
Festuca	12.25	9.73	1	3	2	5	5
Agropyron	7.25	4.55	12	9	5	3	2
Centaurea	3.91	1.23	8	8	14	7	7
Total	76.07						

TABLE 3. Spearman's correlation coefficients ([a] denotes $P < 0.05$, [b] denotes $P < 0.10$) comparing five estimated winter diets of elk on the Threemile Wildlife Management Area (e.g., the KNAP86 diet [Lavelle 1986] pertains to the 1986 winter; Table 1).

	Diet				
Diet	KNAP86	KNAP90	GRAS91	GRAS93	Average
Potentially affected x potentially affected by knapweed removal					
GRAS90			0.335	0.423	
GRAS91				0.610[a]	
					0.46
Unaffected (KNAP86) x potentially unaffected by knapweed removal					
KNAP90	0.517[b]				
					0.52
Potentially affected x unaffected or potentially unaffected by knapweed removal					
GRAS90	0.225	0.526[b]			
GRAS91	0.110	0.308			
GRAS93	-0.005	-0.005			
					0.19

TABLE 4. The influence of snow depth (cm) and julian day (beginning 1 December) on winter counts of elk tracks and feeding craters, as indicated by Pearson correlation coefficients and multiple linear regression, Threemile Wildlife Management Area ([a] denotes $P < 0.05$, [b] denotes $P = 0.07$).

			Correlation		Regression	
Year	N	Dependent Variable	Snow	Day	F	R^2
1990	5	Tracks	0.26	0.54	—	—
		Craters	0.04	0.33	—	—
1991-1993	13	Tracks	-0.44	-0.59[a]	3.54[b]	0.41
		Craters	-0.17	-0.06	0.14	0.03
1990-1993	18	Tracks	-0.26	-0.18	0.64	0.08
		Craters	-0.33	0.19	2.08	0.22

TABLE 5. Comparative indications of winter elk presence and abundance on the old-field grassland of Threemile Wildlife Management Area.

Method	Previous Studies	This Study
Subjective assessment	Light elk use, occasionally moderate or no use (Beall 1974). Few elk, minimal use (Lavelle 1986).	Moderate-heavy use, based on the criteria of Beall (1974).
Pellet-group (PG) count	14 PG/ha (Hakim 1975)	184 PG/ha
Largest elk group observed	17 (Lavelle 1986) 11% of N^a 25, approx. (Beall 1974) 17% of N^b	68 (18 Jan 1993) 31% of N^c
Largest elk group, judging from tracks		95 (31 Dec 1989) 43% of N^c

N^a = 149 elk estimated in the Threemile population, 1986-1989; N^b = 148 elk estimated, 1971-1973, by Beall (1974); N^c = 220 elk estimated, 1990-1994

Annual trend counts of the Threemile elk population averaged 47% higher ($t = -2.70$, $P = 0.074$) during March-April 1990, 1991, 1993 and 1994 ($\bar{x} = 165$, $SD = 38$) than during 1986-1989 ($\bar{x} = 112$, $SD = 26$). Similar methods in comparable cover and terrain in the Elkhorn Mountains detected 74.7% of 87 marked elk (R. M. DeSimone pers. comm.), providing a correction factor to suggest the Threemile population averaged about 220 elk in 1990-1994 and 149 elk in 1986-1989. Beall (1974) used marked animals and multiple census counts to obtain annual estimates of 127-168 elk in the Threemile population in 1971-1973.

Elk numbers and indicators of use in the old-field increased beyond proportions explained solely by the population increase documented during this study. I observed 31-43% of the estimated Threemile population in the old-field, compared with reports equivalent to 11-17% of the population before knapweed removal (Table 5). Therefore, I rejected H_0IV, and concluded that factors associated with knapweed removal attracted elk to the old-field, presumably from elsewhere within the winter home range of the Threemile population (H_aIV).

Discussion

Factors associated with knapweed removal in the old-field apparently attracted elk numbers equivalent to 14-32% of the Threemile population, in addition to the estimated 11-17% of the population that used the old-field before knapweed removal (Table 5). By definition, this distributional shift toward the old-field (H_aIV) also decreased elk-days of use elsewhere across the winter home range. Although otherwise unaffected by knapweed removal, elk remaining in traditionally used habitats away from the old-field may have benefitted from reduced competition for limited resources (e.g., Bartmann et al. 1992). Thus, elk redistribution in response to knapweed removal may have been analogous to a winter population reduction approaching 14-32%. Previous studies have associated changes in population density with changes in the population dynamics of elk (Buechner and Swanson 1955) and red deer (*C. e. scoticus,* Clutton-Brock et al. 1982:259-285).

Moreover, knapweed removal expanded foraging options for the estimated 31-43% of the elk population (Table 5) which used the old-field (H_aI). A corresponding dietary response to factors linked with knapweed removal was detected in all three winters (H_aII). This dietary response was indicated by fecal analysis despite high environmental variability which may have overwhelmed this study's power to detect more subtle dietary changes of potential biological significance (White 1983). Environmental variability was high because: (1) knapweed removal modified only about 5% (i.e., old-field) of the winter home range of free-roaming elk, (2) few forage taxa occurred in the old-field compared to the remainder of the winter home range, and (3) plant fragments in feces collected in the old-field may have been ingested at distant feeding sites several days before defecation (Nelson and Leege 1982). I infer high biological significance from the fact that a dietary response attributable to knapweed removal could be distinguished from the influences of these uncontrolled variables. Likewise, Wickstrom et al. (1984:1299) concluded that management practices affecting vegetation on winter ranges are likely to have profound impact on ungulate foraging efficiency during the season when energy balance is especially critical.

The KNAP90 and GRAS90 diets were rank correlated (Table 3). This was an expected result of sampling both diets from the same population during the same winter (Table 1), and did not diminish the importance of observed differences between these diets which were attributed to factors associated with knapweed removal (Table 2). Further, the significant rank correlation between the KNAP90 and KNAP86 diets, and a lack of correlation between the GRAS90 and KNAP86 diets (Table 3), promoted confidence in the KNAP86 diet as a valid baseline for assessing dietary changes linked with knapweed removal. Therefore, the purpose for estimating the KNAP90 diet was served.

Only one treatment site and one control site were compared. Therefore, this study lacked replication, which precluded the use of inferential statistics to test for treatment effects (Hurlbert 1984). The t-test in Figure 3 indicated that crater counts differed between sites while track counts did not. From this, I concluded that elk foraged more on the treated site than on the control site, though they walked through both sites indiscriminately. This, considered with the other results of this study, led me to subjectively conclude that factors associated with knapweed removal (i.e., the treatment itself) caused the observed foraging

response. Replication was sacrificed to evaluate a treatment of sufficient size for assessing management applications while simultaneously confining environmental variation to that found within the range of a single elk population. Replicated experiments, as well as observational studies such as this one, are needed to advance ecological understanding (Eberhardt and Thomas 1991).

Factors associated with knapweed removal were most attractive to foraging elk in 1990 (H_a III, Figure 2). This initial attraction appeared to override the effects of snow depth and winter duration which influenced foraging activity in 1991-1993 (Table 4). Knapweed removal may have attracted elk because: (1) knapweed was removed, (2) grass standing crop increased, and/or (3) forage quality characteristics of the grasses improved. Knapweed and grass standing crops were consistent across all winters after knapweed removal and could not explain a higher attraction in 1990. However, forage quality may have been higher in 1990 due to: (1) a short-term fertilizer effect caused at the time of treatment by a release of nutrients previously occupied by living knapweed plants (Harvey and Nowierski 1989), and/or (2) a one-time occurrence of abundant green grass on the winter range.

More grass litter was present in the old-field in 1991-1993, but probably did not explain the abrupt drop in foraging activity observed in 1991. Jourdonnais and Bedunah (1990) observed less elk feeding use of rough fescue (*F. scabrella*) plants with dense standing litter. While rough fescue produces dense tufts of persistent standing litter, the nontufted grasses prevalent in the old-field (e.g., bluegrasses and bromes) did not. By ocular estimate, elk consumed about 35% of the grass standing crop on the transects before 25 February 1990, and the remaining unconsumed foliage tended to flatten, presenting no apparent obstruction to elk feeding on current year's growth in the winter of 1991.

The effects of knapweed removal appeared to continue attracting elk foraging activity and influencing winter diets in 1991-1993 (Figure 2; Tables 2, 3, and 5). Prior to knapweed removal, a high density of coarse, persistent, knapweed stems may have deterred elk from grazing the scattered grass plants in the old-field, comparable to the effect of standing dense litter on elk use of rough fescue (Jourdonnais and Bedunah 1990). Additionally, grass production gains concurrent with knapweed removal may have increased winter foraging efficiency. Wickstrom et al. (1984) reported that dry matter intake rate decreased when elk grazed grass stands with forage biomass levels below a threshold of about 1,500 kg/ha, and they concluded it was unprofitable for elk to graze grass swards of low productivity, regardless of digestibility. Applying their results to the present study, the increase from about 700 kg/ha grass to 1,600 kg/ha (Carpenter 1986) caused by picloram treatment may have exceeded a production threshold important in the foraging energetics of wintering elk.

The foraging response of elk might have been stronger in 1991-1993 if native bunchgrasses were more abundant in the old-field. Although bluegrasses comprised 18% of the winter elk diet in the Elkhorn Mountains, Gordon (1968) reported that elk did not use cured bluegrass foliage. The cured foliage of Idaho fescue and bluebunch wheatgrass were the primary winter foods reported by Gordon (1968). Likewise, Threemile elk were attracted to the bluegrass dominated old-field when grasses were predominately green in 1990, but foraged less in the old-field when bluegrasses were predominately cured in 1991-1993.

Conclusions and Recommendations

Elk populations in Montana are at twentieth century highs (Firebaugh 1993), coincident with the increase and spread of knapweed (Lacey 1989). Although existing habitat could support more elk, lower population objectives are necessary for compatibility with competing human uses of the land (Wildl. Div., Elk Manage. Plan, MDFWP, Helena, 1992). Thus, the question of whether existing knapweed infestations on elk winter ranges limit ecological carrying capacity is somewhat academic when elk numbers are limited to a lower economic carrying capacity, as defined by Caughley (1979).

Nevertheless, the results of this study are pertinent to elk management in two respects. First, continued spread of knapweed beyond current distributions, and increased knapweed densities within existing stands, should concern managers of grassland winter ranges who strive to maintain the current productivity of associated elk herds. Second, removal or thinning of existing knapweed stands in favorable foraging habitats may attract

elk, potentially yielding similar habitat and herd enhancement results as fertilizing, burning, and prescribed cattle grazing (Rowland et al. 1983, Skovlin et al. 1983, Jourdonnais and Bedunah 1990, Frisina 1992).

It is unknown if the elk foraging response in the old-field was representative of the response managers should expect from knapweed removal on typical bunchgrass winter ranges. Recovery rates of native rangelands may be depressed by historical use (Willms et al. 1985), which would remain a factor regardless of knapweed removal. Extrapolating the results of the present study, knapweed removal would elicit the largest foraging response where preexisting densities of both knapweed and preferred forage grasses were high. Further, at least a portion of the elk response to knapweed removal in the old-field was likely attributable to a short-term forage quality increase in the first winter following picloram treatment. The coincidence of massive knapweed mortality with adequate rainfall was probably an important determinant of the observed forage and elk response in the first winter. Managers hoping to replicate these conditions should apply picloram or other appropriate herbicides as soon as the range becomes snow-free in spring to take full advantage of available moisture in the first growing season.

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Agricultural Practices Affect Botfly (Cuterebridae) Prevalence in Gray-tailed Voles (*Microtus canicaudus*)

Abstract

We examined the effects of an organophosphorous insecticide (azinphos-methyl) and mowing of alfalfa on larval botfly (Cuterebridae) prevalence in gray-tailed voles (*Microtus canicaudus*) in enclosed populations. Twelve of 24 enclosures were mowed, and three concentrations of an insecticide (Guthion 2S®) were applied three weeks after mowing. We captured 3,529 voles between 17 July and 27 August 1993, and 88 had at least one botfly parasite (overall prevalence = 2.5%). We found the prevalence of botflies in male voles (3.25%) to be significantly greater than in females (1.82%; $X^2 = 6.06$, $P < 0.015$). The interaction of mowing and insecticide application was a significant factor in determining botfly prevalence ($X^2 = 5.88$, $P < 0.055$); prevalence of botfly infection was lower in mowed than in unmowed enclosures except at the highest insecticide concentration, which reduced the number of infections in both mowed and unmowed enclosures. We suggest the reduction in botfly prevalence resulted from the direct effect of both mowing and insecticide application on adult botflies and botfly eggs, whereas differences in prevalence between genders was related to the voles' activity patterns.

Introduction

Botfly parasites of the family Cuterebridae are common among new world rodents, and may affect activity patterns (Smith 1978a) and survival of the host (Miller and Getz 1969, Boonstra et al. 1980). Botfly larvae exert varying physiological stresses associated with subcutaneous feeding (Smith 1977) that may cause a decrease in non-maintenance activity (Smith 1978a) or survival (Boonstra et al. 1980) or increase susceptibility to predation (Smith 1978b), but the infections usually do not cause death of the host. Thus, parasite and host have evolved physiological adaptations permitting survival of both (Timm and Cook 1979).

No studies have examined how agronomic activities may alter botfly-host relationships. Agricultural practices may alter botfly habitat, causing a reduction in botfly populations or botfly egg viability and thereby reducing their prevalence in host populations. Botfly infection occurs when the host comes in contact with eggs, but except for host-specific site oviposition in pocket gopher (*Thomomys talpoides*) burrows (Capelle 1970) and dusky-footed woodrat (*Neotoma fuscipes*) houses (Catts 1967), most evidence suggests oviposition in the immediate area of host activity (Baird 1974). Our objective was to examine the effect of an organophosphorus insecticide and mowing on the prevalence of botfly in gray-tailed voles (*Microtus canicaudus*). We hypothesized that mowing and insecticide application would have no effect on botfly prevalence.

Materials and Methods

This study was conducted in the Willamette Valley, at the Oregon State University Hyslop Crop Sciences Field Laboratory (~10 km north of Corvallis, Oregon [44° 38' N; 123° 12' W]). The site contained 24 0.2-ha enclosures, bordered by galvanized sheet metal ~1 m above and ~0.6 m below the ground surface. All enclosures were planted with alfalfa (*Medicago sativa*) in the spring of 1991. A 1-m-wide strip along the inside perimeter of each fence was regularly mowed to minimize vole activity near the perimeter and reduce activity near abnormally high concentrations of insecticide dripping down the fence (Edge et al. 1996). Each enclosure had seven breeding pairs of gray-tailed voles introduced in April 1992, and on 4-6 April 1993, enclosed populations were mixed to increase genetic variability and densities were equalized.

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Each enclosure contained 100 traps; 75 Sherman live traps (7.5 x 9.5 x 25.5 cm; model LFATG; H. B. Sherman Traps, Inc., Tallahassee, Florida) and 25 pitfall traps (45 cm deep, 15 cm in diameter). Traps were arranged in a 10 x 10 grid, each 5 m apart with pitfalls located at all odd stations (i.e., 1-1, 3-3, 9-9). When not in use, pitfall traps were covered and Sherman traps were locked open. Four or five days before the start of each trap period, all Sherman traps were prebaited with oats. When trapping, all traps were opened in the evening; Sherman traps were baited with oats while pitfall traps were not baited. Traps were checked the following morning, and closed or covered during the day.

We trapped four consecutive nights every two weeks (trap period) from 18 May through 27 August 1993. All trapped animals were sexed, weighed, and ear-tagged, and the number and location of botfly larvae present were recorded. Animals with multiple simultaneous botfly infections were each counted as one infected individual during each trap period. Animals with botfly infections in the same location during consecutive trap periods and no larval exit wound were considered infected animals only during the earlier of the two trap periods.

Four enclosures were randomly assigned to each of six insecticide-mowing treatment combinations: 0.0 kg/ha-mowed, 0.88 kg/ha-mowed, 3.61 kg/ha-mowed, 0.0 kg/ha-unmowed, 0.88 kg/ha-unmowed, and 3.61 kg/ha-unmowed. Enclosures were mowed on 22 June 1993 to a height of approximately 15 cm; cuttings were not removed. The insecticide Guthion 2S® (azinphos-methyl; *O,O*-dimethyl *S*-[(4-oxo-1,2,3-benzotriazine-3(4*H*)-yl) methyl]ester; Mobay Corporation, Agricultural Chemical Division, Kansas City, Missouri, USA) was applied on 14 July 1993 by a licensed applicator using a four-wheel all-terrain vehicle pulling a trailer tank with 7.6-m spray booms (Schauber et al. 1995). Enclosures were sprayed in order of increasing application rate; controls received an equal volume of water.

Only animals trapped during the period of botfly infection, from 17 July to 27 August 1993 (four trap periods), were used in this analysis. We combined replicate enclosures for statistical analysis because there were insufficient botfly larval-infected voles in all enclosures throughout the study. We used logistic regression and the Statistical Analysis System (SAS Institute, Inc. 1987) to identify the explanatory variables (gender, mowing, insecticide, and interactions) accounting for the prevalence of botfly infections.

Results

Of the 3,529 voles we captured between 17 July and 27 August 1993, 88 had at least one botfly parasite (overall prevalence = 2.5%). Mean intensity of botfly infections was 1.4 parasites per host, and ranged from one to four; 76% of the infected animals had one larval parasite, while 16% had two, 2% had three, and 6% had four. The subcutaneous locations of the larval parasites were predominantly inguinal (79%); other locations included the chest and stomach (12%), hindquarters (8%) and face (1%).

Botfly prevalence was affected by both agricultural practices and gender of the host. Prevalence in male voles (3.25%; n = 1,663) occurred at almost twice the rate as in female voles (1.82%; n = 1,866) (X^2 = 6.06, 1 d.f., $P < 0.015$). The interaction of mowing and insecticide application was also a significant factor affecting botfly prevalence (X^2 = 5.88, 2 d.f., $P < 0.055$). In control and 0.88 kg/ha concentration enclosures, the number of infected voles in mowed enclosures (n = 1,880) was considerably lower than in unmowed enclosures (n = 1,649). In the unmowed 3.61 kg/ha concentration enclosures, there was a sharp decrease in the number of infected animals, resulting in almost no difference in the prevalence of botfly between the mowed and unmowed enclosures (Figure 1).

Discussion

Variations in the prevalence, location, and intensity of botfly larvae may reflect differences in the life history of the host or botfly, or they may result from seasonal differences in infection or from differential survival of the host. Many studies of botflies in small mammals have found higher prevalence of the parasite than we found in this study. Getz (1970) found 16% of adult meadow voles (*M. pennsylvanicus*) in unmowed habitat infected. Studies of deer mice (*Peromyscus* spp.) have found 12-40% of adult males and 16-38% of adult females infected (Miller and Getz 1969, Seaman and Nash 1976). We found the majority of botfly larvae in gray-tailed voles in the inguinal

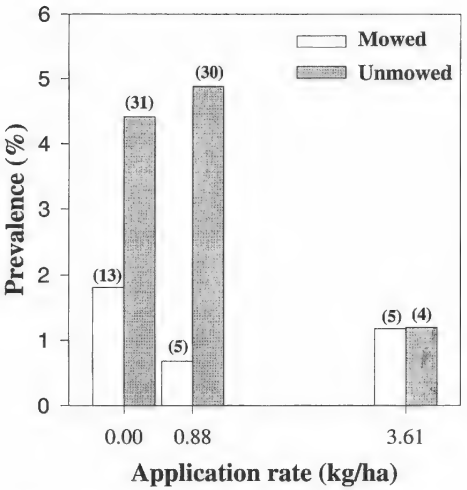

Figure 1. Prevalence of botfly larvae in gray-tailed voles by mowing and insecticide application rate. Numbers in parentheses are number of animals infected.

region, whereas larval infections of meadow voles in Wisconsin were in the same body regions, but were more evenly distributed: 37% inguinal, 26% sides, 22% chest, 10% back, and 5% head (Getz 1970). Infections in deer mice have been found solely on their sides and backs (Llewellyn 1978), predominantly on their rump (Seaman and Nash 1976), and predominantly inguinal (Miller and Getz 1969). Differences in the life histories of botflies or host physiology may account for such variation (Catts 1982), but the health and activity of the host may also influence variation in warble location.

Although most individual small mammals usually bear only one larval infection at a time, multiple simultaneous botfly infections have been found in meadow voles (Getz 1970), deer mice (Seaman and Nash 1976), and gray-tailed voles (this study). However, the number of individuals with multiple infections is relatively low, probably because of decreased activity (Smith 1978a) or survival (Boonstra et al. 1980) of individuals with more than one warble.

Physical and chemical habitat manipulation may reduce the activity and survival of both the host and the botfly. In our study, the difference in botfly prevalence between mowed and unmowed enclosures, and the decline in prevalence in unmowed high-dose enclosures, suggest that mowing and insecticide application each has a negative effect on the incidence of botfly infection. In a uniformly non-woody marsh in Wisconsin, Getz (1970) reported higher prevalence of botfly in the unmowed than in the mowed habitat, and suggested that the presence of a litter layer in the unmowed habitat was the main physical difference between the two habitats. All enclosures in this experiment were mowed in 1992; thus differences in the litter layer presumably would not account for higher prevalence in unmowed enclosures than in mowed enclosures. The differences in prevalence between mowed and unmowed enclosures was possibly the result of a change in the micro-climate surrounding oviposited eggs. Mowing may have subjected botfly eggs to increased direct sunlight resulting from reduced cover. Botfly eggs in environments with temperatures >35° C and in environments with low humidity were both found to have reduced survival (Catts 1967). Whereas the individual effects of mowing and insecticide applications cannot be isolated, the reduction in botfly prevalence could be the result of increased mortality of adult botflies and oviposited eggs, and reduction of favorable botfly habitat for oviposition.

Insecticide effects on botfly prevalence may be a function of vegetation density. In unmowed enclosures, alfalfa structure and height affected the vertical distribution of insecticide, resulting in 70-87% decreases in concentrations at the soil surface and on the lower vegetative structures (Bennett et al. 1994) where botflies oviposit. In mowed enclosures, the insecticide reaching the lower layers of vegetation significantly reduced arthropod communities (J. Miller, Department of Entomology, Oregon State University, unpublished data) and was probably sufficient to kill botfly eggs. In 3.61 kg/ha concentration enclosures, the concentration of insecticide near lower plant structures was probably sufficient to kill botfly eggs and adults regardless of vegetation cover.

The relationship between the voles' gender and the prevalence of botfly larvae may be related to size of home range and activity patterns of the host. Male gray-tailed voles have significantly larger home ranges than females (Wolff et al. 1994). Because botflies generally lay eggs at multiple sites in scattered patterns (Catts 1967, Baird 1974), the probability of infection should increase with increased range of activity.

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Initial Response of Understory Plant Diversity and Overstory Tree Diameter Growth to a Green Tree Retention Harvest

Abstract

The increasing use of harvest techniques other than clearcutting in forests west of the Cascade mountains has created an urgent need to understand the effects of these practices on ecosystem species composition and structure. One common alternative, "green tree retention" (GTR), leaves some live trees on a harvest site to more closely mimic a moderate-intensity fire or wind disturbance. We examined the response of understory plant diversity and basal area increment of retained overstory trees after sixteen months and six years, respectively, in GTR cuts. Understory species cover was sampled on three adjacent treatment areas in the Seattle City Watershed, Washington: a clearcut, a dispersed green tree retention and the intact sixty-five year old forest. The change in basal area increment on dispersed green tree retention cuts was sampled with increment cores collected in six stands and two uncut control stands in the Wind River and H.J. Andrews Experimental Forests in Washington and Oregon, respectively. Herb and shrub species richness and evenness were significantly higher in the green tree retention cut than in the other two understory treatments. Although overall species composition of the GTR was closer to the clearcut than the forest, the GTR retained more species and cover of shade-tolerant plants important for maintaining understory diversity as canopy closure reduces understory light. While the basal area increment response of retained trees varied between stands, the average response for all stands for a six year period following harvest was a 15% reduction in increment growth compared to the control stands. Additional study is needed to determine the persistence of these effects and how basal area growth response varies as a function of tree size and age.

Introduction

In the Pacific Northwest a fundamental change in forest management techniques has occurred in the last several years on Federal, State and some private lands. These changes are often collectively termed "new forestry" (Franklin 1989; Gillis 1990; Hopwood 1991), "new perspectives" (Salwasser 1990; Kessler et al. 1992) or "ecosystem management" (Eubanks 1989; Grumbine 1994; Salwasser 1994). Although variously named, the common goal of all these approaches is to integrate efforts to sustain biological diversity and long-term ecosystem health into forest resource planning and timber management (Lertzman 1990; Swanson and Franklin 1992). One particular change is the increasing use of alternative cutting techniques in forests west of the Cascade mountains of Washington and Oregon where the most common practice has been clearcut harvesting followed by slash burning. One alternative method, referred to here as "green tree retention" (GTR), involves leaving approximately five to 60 large, live trees per hectare on a logging site to persist through the next rotation to increase the structural diversity of the regenerating stand. This structural diversity is intended to retain some later seral conditions such as a multi-layered canopy, provide a future supply of large snags and down logs, and increase microsite variability for a more diverse understory (Franklin 1989; Gillis 1990). In theory, green tree retention harvests are designed to more closely mimic conditions following a moderate-intensity wind or fire disturbance and thereby change the impact of logging on ecosystem structure and function.

As a harvest technique, the concept of "green tree retention" is not a new silvicultural practice. In the Pacific Northwest, alternatives to clearcutting have been proposed and experimentally tried throughout the century under such names as selective harvest (Kirkland and Brandstrom 1936), seed tree cutting (Isaac 1956) or irregular shelterwood (Smith 1986, USDA Forest Service 1979). Although the rationale behind each of the methods may have differed, the common result

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has been to leave some live trees on site after initial harvest. Green tree retention, therefore, may not be a "new" forestry, but it is being applied on a larger scale than previous silviculture alternatives west of the Cascade Mountains. The U.S. Forest Service and Washington State's Department of Natural Resources have adopted green tree retention as a standard harvest practice (Robertson 1992; Washington Forest Practices Board 1993) and some private companies are experimenting with its use (Washington Forest Protection Association 1995). While green tree retention harvests are becoming more common, little is known about how this alternative silviculture will affect ecosystem processes or the structure and composition of the forest community. Research is needed on fundamental ecosystem responses including impacts on the understory plant community and the retained overstory trees.

Current computer models and retrospective studies of multi-cohort stands can provide only limited information on how green tree retention will affect either growth of the overstory trees or the understory plant community. Predicting growth changes in overstory trees using computer models such as DFSIM (Curtis et al. 1981) and ORGANON (Hann et al. 1992) would be difficult because the model algorithms are predominantly based on growth and yield information gathered from even-aged, short rotation practices. Another approach would be to sample existing stands which through past disturbance or silvicultural experiments approximate a green tree retention stand condition. However, most existing multi-cohort stands in western Oregon and Washington have a variable density of residual trees and comparisons between dissimilar sites would be difficult (Thomas et al. 1993).

The effects of a green tree retention harvest on understory diversity are also difficult to predict from existing studies. Changes in understory community composition during natural succession (Spies 1991) and in response to a clearcut and slash burn disturbance (Halpern 1988, 1989) have been studied. However understory plant succession and diversity are influenced by both life history traits of the plants in the community and the disturbance intensity (Connell and Slatyer 1977; Noble and Slatyer 1980; Halpern 1989). By leaving trees on a site, green tree retention attempts to change the nature and intensity of the logging disturbance. To assess whether this change in disturbance affects the understory community, vegetation response on green tree retention sites should be studied. It is important to understand the response of both overstory trees and understory plants to alternative silviculture because these processes will affect the structural and functional development of the regenerating forest.

In this paper we examine overstory tree and understory plant response in the first few years after green tree retention harvests. To assess the response of overstory trees, we located the oldest dispersed green tree retention cuts available (harvested in 1988) and compared the change in mean basal area increment for these stands with adjacent stands which had not been cut. To examine the impact of green tree retention on the understory community we compared species composition, richness and evenness on a small, relatively homogenous site where an experimental harvest produced a clearcut (CC), dispersed green tree retention (GTR), and the original forest (FOR) in close proximity. While this study provides information on the initial response of a particular community, responses are likely to vary between sites and with different harvesting methods. This study limits comparisons to a few sites in close proximity and results should not be generalized to conditions for all green tree retention harvests.

Study Areas

The response of understory plants to different harvest methods was studied in the Seattle City Watershed (also known as the Cedar River Watershed), sixty kilometers east of Seattle, Washington. The 26.9 hectare site had been harvested in the summer of 1992, producing three contiguous units: an 8.1 hectare clearcut (all trees felled), an 18.7 hectare dispersed green tree retention (27 live trees per hectare), and a 0.1 hectare patch of retained trees (no cutting). The patch was not included in the analysis because its small size and singularity made understory comparisons unreliable. A survey of the understory community on the CC and GTR sites was not made before harvest. However, an adjacent intact forest of 65 year-old trees was included to compare understory composition and diversity between clearcut, green tree retention and no harvest treatments. Although the study area before harvest was fairly homogenous (McCalmon pers. comm.) differences in

the present understory composition may be partially due to pre-harvest differences in understory composition between the adjacent sites.

Basal area, species composition and stocking density of the GTR and clearcut areas were the same as the intact forest before they were cut (City of Seattle Watershed, unpublished data). The study area is flat and at an elevation of 480 meters. The three treatment sites are within 300 meters of each other and represent the *Abies amabilis/ Vaccinium membranaceum* association (Henderson et al. 1992). The average tree diameter in the intact forest and before harvest in the clearcut and green tree retention units was 37 cm, with a total basal area of 66 m^2/ha. The species mix on the site was 65% western hemlock (*Tsuga heterophylla*), 19% Douglas-fir (*Pseudotsuga menziesii*) and 16% Pacific silver fir (*Abies amabilis*). On both the clearcut and green tree retention sites logs were yarded over skid roads using tractors. The green tree retention and clearcut areas were planted in 1993 with a mix of noble fir (*Abies procera*), Douglas-fir and Sitka spruce (*Picea sitchensis*) at 740 trees/ha. The understory plant cover was sampled in September of 1993, 16 months after harvest.

The retained green trees at the Seattle City Watershed site were not sampled for changes in basal area increment because only 16 months of growth response could be examined. Instead, sample stands for overstory diameter response were selected from the oldest green tree retention cuts in the Pacific Northwest which we could find. Four stands in the H.J. Andrews Experimental Forest east of Eugene, Oregon, were selected. Three of these stands were cut in 1988 and logs were hauled to the landings with tractors. The density of leave trees at the three sites was 20, 43 and 45 trees per hectare of mature Douglas-fir. Although sites did have variable retention density, only stands with low densities were used in this study to minimize the effects of stem competition. Retained trees at all sites were widely dispersed and the distance between adjacent crowns was five meters or more. Mortality of retained overstory trees appeared low but was not systematically sampled. The three GTR sites had been burned following harvest and planted with Douglas-fir seedlings. A fourth undisturbed stand, adjacent to the green tree retention stands, was sampled as a control. The dominant Douglas-fir trees at all sites were 120-140 years old, and average site diameter ranged from 65 to 78 cm. The four sites are in *the Tsuga heterophylla/Rhododendron macrophyllum/ Berberis nervosa* plant association (Franklin and Dyrness 1988), range in elevation from 700 to 900 meters and are on moderate slopes of 10-25°.

Tree diameter increment cores were also collected on four stands near the Wind River Experimental Forest north of Stevenson, Washington. Three of these stands were harvested with tractors in 1988 and planted with Douglas-fir. Retention trees at the three sites averaged 16, 20 and 25 trees per hectare of 130-145 year-old, Douglas-fir. Retained trees on all three sites were widely dispersed and tree crowns were separated by at least five meters. A fourth control stand adjacent to the green retention sites was also sampled. All sites are fairly level, near 600 meters in elevation and in the *Tsuga heterophylla/ Polystichum munitum* plant association (Franklin and Dyrness 1988).

Methods

Understory vegetation in the uncut forest, clearcut, and green tree retention was sampled with 180 plots taken along randomly placed transects. Plots were placed along three 100 meter transects using a random number generator for values between 0 and 100. At each plot location a two by two meter frame, gridded into 49 squares, was placed over the vegetation. These smaller units, each representing approximately two percent cover, were used to improve the accuracy of visually estimating species cover. Planted trees and coarse woody debris from the logging operation were not included in the analysis. All herbs, shrubs and naturally regenerating trees were identified using Hitchcock and Cronquist (1973) nomenclature. Moss was not identified to genus and species, and bluegrasses (*Poa* spp.), rushes (*Juncus* spp.), wintergreen (*Pyrola* spp.), and willow (*Salix* spp.) were identified only to genus.

Species diversity was analyzed using two measures, richness and dominance (Magurran 1988). Richness was examined at two spatial scales; the total number of species found in each treatment, and the mean number of species per plot. The mean species richness per plot was compared using single-factor ANOVA (Zar 1984). Dominance was evaluated to assess whether a treatment's

understory was strongly dominated by a few species or, inversely, whether species were more evenly distributed. To evaluate dominance in understory diversity, the Berger-Parker index (d) was used:

$$d=N_{max}/N$$

N_{max} = total cover of the most abundant species

N= total cover of all species

The conventional practice of adopting the reciprocal form of the measure (1/d) was employed so that the index increases with increasing evenness (Magurran 1988). In this conventional form, high Berger-Parker values indicate cover amongst species is more evenly distributed, and low values indicate dominance by a single species.

Analyzing understory species by their functional role can also provide insight into plant community dynamics and the seral development of a site. Following disturbance in the Pacific Northwest, species richness in forest understory communities greatly increases (Franklin and Dyrness 1988; Schoonmaker and McKee 1988). At the time of sampling, 16 months after harvest, many understory plants are ruderal, non-forest species which rapidly colonize harvest sites. With seral development these invasive species rarely persist through the low-light conditions of canopy closure, and on-site residual forest species regain site dominance. An understory's composition of invasive and residual species can indicate the disturbance intensity and community resilience of a site (Halpern 1988). To examine each treatment's response, species were identified as either residual or invasive depending on whether they are characteristic of undisturbed forest or are commonly restricted to localized disturbed sites. In Pacific Northwest forests this distinction is based on function rather than plant origin because several invasive species are natives (e.g. salmonberry (*Rubus spectabilis*)). Species were classified as invasive or non-invasive following descriptions in regional plant taxonomic guides (Hitchcock et al. 1969; Hitchcock and Cronquist 1973; Klinka et al. 1989; Pojar and McKinnon 1994) and previous studies (Dyrness 1973; Halpern 1988; 1989).

Classifications of the understory data were made using TWINSPAN, a FORTRAN program which uses reciprocal averaging to make divisive classifications of species and plot samples (Hill 1979). The only non-standard option employed in the TWINSPAN program was a change in the pseudospecies cut levels from five (the default) to six to better reflect typical abundance levels at the sample sites (Hill 1979). In field sampling, all species present were recorded even if their coverage was below the minimum coverage value of 0.5%. These trace species were given a coverage value of 0.1%, and a pseudospecies cut level of 0.2% was added to the other values (i.e. 0, 2, 5, 10, and 20) to include the trace species in the classification divisions.

Overstory trees were sampled within each stand by randomly selecting thirty Douglas-fir trees. Each tree was cored on its uphill side at breast height. Cores were mounted, sanded, and measured under a dissecting microscope using the TRIM (Tree Ring Increment Measurement) computer program. Increment cores for each of the eight stands were analyzed separately for the H.J. Andrews and Wind River Experimental Forests areas. The annual change in basal area increment for each tree was standardized by comparing the post-GTR growth each year from 1988 to 1993 to the mean pre-GTR growth for 1983 to 1987 for each tree. This procedure helps control for variation between trees and in site quality between stands (ex. Chen et al. 1992). The annual response for each stand from 1988 to 1993 was calculated using the mean and standard error of the change in basal area increment for all thirty trees.

Results

Understory

Total species richness was highest in the GTR (42 species present), followed by the clearcut (32) and the forest (20) (Table 1). Plot-level species richness (mean number of species in each 4 m^2 sample) was significantly different between treatments ($F_{0.05\,(1),2,179}$= 3.05, P<0.005). Most of the GTR and clearcut's higher richness was due to a greater number of herbs, grasses and shrubs. Both the forest and the GTR had twice the number of fern species of the clearcut.

The most abundant cover in the forest is moss which accounted for 91% of total understory cover, giving a Berger-Parker value of 1.1. The forest's species richness and evenness values may be biased downward because the study did not identify different moss species. Classifying moss to species, however, may not have significantly changed the relative differences in species diversity between

TABLE 1. A comparison of species richness and evenness between the three samples sites, intact forest (FOR), clearcut (CC) and green tree retention (GTR). Species evenness values are for the Berger-Parker (B.P.) index. Higher B.P. values indicate greater evenness. Common and scientific names for the dominant species acronyms are given in Table 2. Acronyms in upper case were classified as invasive and those in lower case as residual.

	FOR	CC	GTR
Total number of species (includes moss)	20	32	42
Herbs	9	15	18
Grasses	0	3	5
Shrubs	3	8	9
Trees	3	3	4
Ferns	4	2	4
Mean richness (# species/plot)	4.9	7.0	10.3
Species evenness (B.P.)	1.1	2.3	9.7
Percent of invasive species cover	0	84	68
Dominant cover species	Moss	SESY	SESY
	Tshe	Tshe	Moss
	Abam	DIPU	Madi
	Madi	RUSP	EPAN

the three treatments because of the large stand-level differences in richness between treatments and because moss was abundant on all treatments.

The most common species in both the GTR and clearcut is wood groundsel (*Senecio sylvaticus*), an invasive exotic commonly abundant following timber harvest (West and Chilcote 1968, Dyrness 1973, Halpern 1989). The clearcut is strongly dominated by wood groundsel as indicated by the low Berger-Parker evenness value of 2.3, while species are more evenly distributed in the GTR with a value of 9.7.

No invasive species were present in the forest. The four plants dominating the understory were all shade-tolerant species: moss, western hemlock, Pacific silver fir, and false lily-of-the-valley (*Maianthemum dilatatum*). The forest contained five species unique among the three treatments: oak fern (*Gymnocarpium dryopteris*), wintergreen (*Pyrola* spp.), Pacific trillium (*Trillium ovatum*), western redcedar (*Thuja plicata*) and Pacific silver fir (Table 2).

Most of the understory cover in the clearcut is from invasive species, particularly wood groundsel, foxglove (*Digitalis purpurea*), and salmonberry (*Rubus spectabilis*). In addition, three grasses and four *Rubus* species contributed to make up most of the total invasive cover. The clearcut did not contain any unique species because all species in the clearcut were also found in the green tree retention cut.

Although more than two thirds of the total cover in the GTR was from invasive species, no single species accounted for more than 10% of the total understory cover. While invasive species increased the GTR's total richness, the relatively high Berger-Parker value of 9.7 indicates species were evenly distributed. The GTR contained six unique species, all considered invasive: wall lettuce (*Lactuca* spp.), rush (*Juncus* spp.), running clubmoss (*Lycopodium clavatum*), bluegrass (*Poa* spp.), black cottonwood (*Populus trichocarpa*) and bracken fern (*Pteridium aquilinum*) (Table 2). The GTR and forest share four shade-tolerant species not found in the clearcut.

Eleven of the 47 species were common to all three treatments (Table 2). Constancy values for these eleven non-invasive species are lowest in the clearcut. Constancy values are a measure of the proportion of sample plots within a treatment on which a given species occurs. Constancy values are used instead of cover values to indicate how common or rare a species is within a treatment. Twenty-one species were found only in the CC and GTR. All 21 were classed as invasive species. Sixteen of the 21 species had higher constancy values in the GTR, reflecting its high plot-level richness and low dominance.

The main division in the TWINSPAN classification of the data by species groups (Figure 1) is between shade-tolerant (left side) and shade-intolerant species (right side). This division also separated most of the residual (lower case) and invasive species (upper case). Six residual species were grouped with the other 27 invasive species. Four of these species, false lily-of-the-valley, foamflower (*Tiarella trifoliata*), ladyfern (*Athyrium filix-femina*), and western swordfern (*Polystichum munitum*) are more tolerant of full sunlight than most residual forest species. Two shade-tolerant species, evergreen violet (*Viola sempervirens*) and queen's cup (*Clintonia uniflora*) were also grouped with the invasive species in the classification because both had high frequency and total cover in the clearcut.

The classification of the plots shows a clear division between clearcut and forest plots at the first level of division (Figure 2). While five of

TABLE 2. List of species found in the three sample stands (CC for clearcut, GTR for green tree retention and FOR for the intact forest) in the Seattle City Watershed, by acronym, scientific and common name. Acronyms in upper case were classified as invasive and those in lower case as residual. The species are organized in five groups: found in all three sample stands, found in both the CC and GTR, unique to the GTR, found in both the GTR and the Forest, and unique to the Forest. No species were unique to the CC or common to only the CC and Forest. Values are species constancy (percent frequency of occurrence for the 60 plots in each treatment).

Acronym	Scientific Name	Common Name	CC	GTR	FOR
Common to CC, GTR and FOR					
atfi	*Athyrium filix-femina*	Lady fern	6.7	31.7	15
clun	*Clintonia uniflora*	Queen's cup	5	16.7	6.7
madi	*Maianthemum dilatatum*	False lily-of-the-valley	31.6	75	51.7
moss	----	Moss	55	91.7	100
pomu	*Polystichum munitum*	Sword fern	10	21.7	21.7
titr	*Tiarella trifoliata*	Three leaved foam-flower	3.3	8.3	5
tshe	*Tsuga heterophylla*	Western hemlock	66.7	70	85
trla	*Trientalis latifolia*	Western starflower	1.6	3.3	3.3
vaal	*Vaccinium alaskaense*	Alaska blueberry	15	41.7	41.7
vapa	*Vaccinium parvifolium*	Red huckleberry	3.3	16.7	33.3
vise	*Viola sempervirens*	Evergreen violet	3.3	5	5
Common to CC and GTR					
AGOR	*Agrostic oregonensis*	Oregon bentgrass	25	30	
ANMA	*Anaphalis margaritacea*	Pearly everlasting	11.7	25	
CAME	*Carex mertensii*	Merten's sedge	30	31.6	
CIAR	*Cirsium arvense*	Canada thistle	3.3	1.7	
DIPU	*Digitalis purpurea*	Common foxglove	48.3	53.3	
EPAN	*Epilobium angustifolium*	Fireweed	43.3	71.6	
EPWA	*Epilobium watsonii*	Purple-leaved willowherb	3.3	8.3	
HYRA	*Hypochaeris radicata*	Hairy cat's-ear	5	6.7	
LUCA	*Luzula campestris*	Many-flowered wood-rush	13.3	36.7	
PREM	*Prunus emarginata*	Bitter cherry	23.3	51.7	
PSME	*Pseudotsuga menziesii*	Douglas-fir	18.3	78.3	
RULA	*Rubus laciniatus*	Evergreen blackberry	3.3	3.3	
RUPA	*Rubus parviflorus*	Thimbleberry	1.6	3.3	
RUSP	*Rubus spectabilis*	Salmonberry	51.7	51.7	
RUUR	*Rubus ursinus*	Trailing blackberry	33.3	36.6	
RUAC	*Rumex acetosella*	Sheep sorrel	1.6	21.6	
SALIX	*Salix* spp.	Willow	5	6.7	
SARA	*Sambucus racemosa*	Red elderberry	50	51.6	
SESY	*Senecio sylvaticus*	Wood groundsel	88.3	85	
SOAS	*Sonchus asper*	Prickly sow-thistle	21.7	21.7	
VEOF	*Veronica officinalis*	Speedwell	5	31.7	
Unique to GTR					
LAMU	*Lactuca muralis*	Wall lettuce		5	
JUNCUS	*Juncus* spp.	Rush		3.3	
LYCL	*Lycopodium clavatum*	Running club-moss		3.3	
POA	*Poa* spp.	Bluegrass		10	
POTR	*Populus trichocarpa*	Black cottonwood		1.7	
PTAQ	*Pteridium aquilinum*	Bracken fern		48.3	
Common to GTR and FOR					
blsp	*Blechnum spicant*	Deer fern		33.3	20
rupe	*Rubus pedatus*	Five-leafed bramble		3.3	1.6
stam	*Streptopus amplexifolius*	Clasping twistedstalk		5	10
vaov	*Vaccinium ovatum*	Evergreen huckleberry		10	15
Unique to FOR					
abam	*Abies amabilis*	Pacific silver fir			63
gydr	*Gymnocarpium dryopteris*	Oak fern			8.3
pyrola	*Pyrola* spp.	Wintergreen			3.3
thpl	*Thuja plicata*	Western redcedar			1.7
trov	*Trillium ovatum*	Western trillium			10

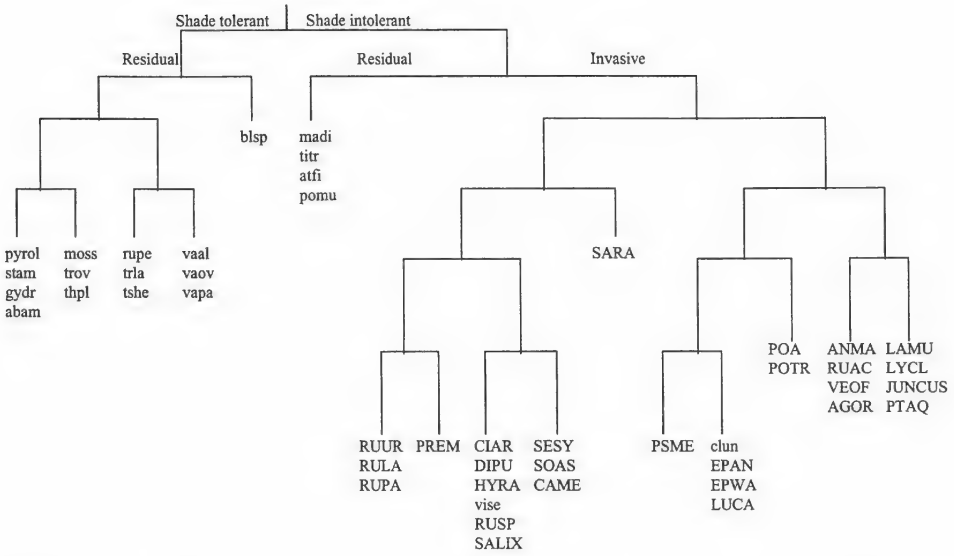

Figure 1. A dendrogram of all species using TWINSPAN. Acronyms in upper case were classified as invasive and those in lower case as residual. Note that most shade-tolerant, residual species are classified in the left branches of the dendrogram and most of the shade-intolerant species are classified in the rightside branches. Common and scientific names for the acronyms are given in Table 2.

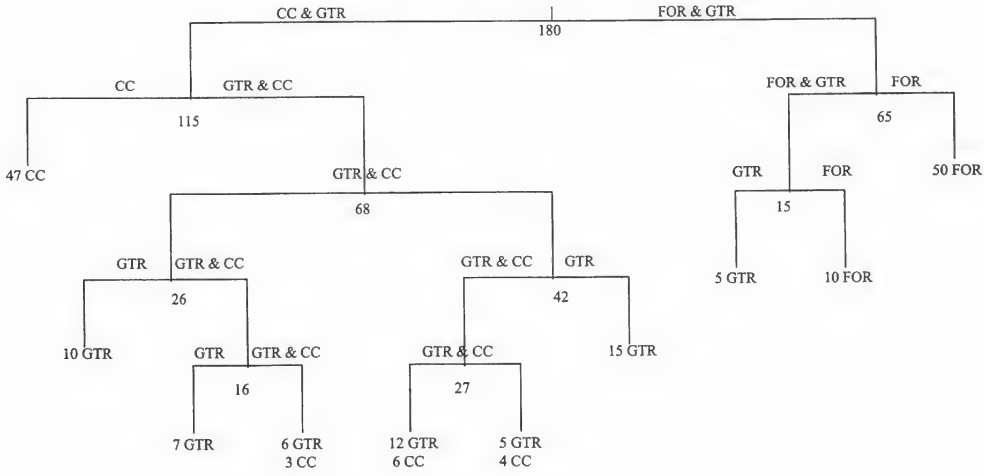

Figure 2. A dendrogram of all sample plots using TWINSPAN. The terminal branches of the dendrogram indicate the number of plots which are from the intact forest (FOR), clearcut (CC), and the green tree retention (GTR). Higher branches indicate which treatments the plots come from and the total number of plots. Classifications were truncated when all plots were in one treatment.

the GTR's 60 plots are classed with the forest plots, most of the GTR plots are grouped with clearcut plots. At the second division level, 55 GTR plots and 13 clearcut plots form a group distinct from most (47) of the clearcut plots. At the lower divisions the 13 clearcut plots are split into three groups shared with 23 GTR plots.

Overstory

Green tree retention stands in both the Wind River and H.J. Andrews areas generally show a decline in basal area increment growth (Figure 3). At Wind River the uncut control stand's annual basal area increment (BAI) has increased an average of 9%

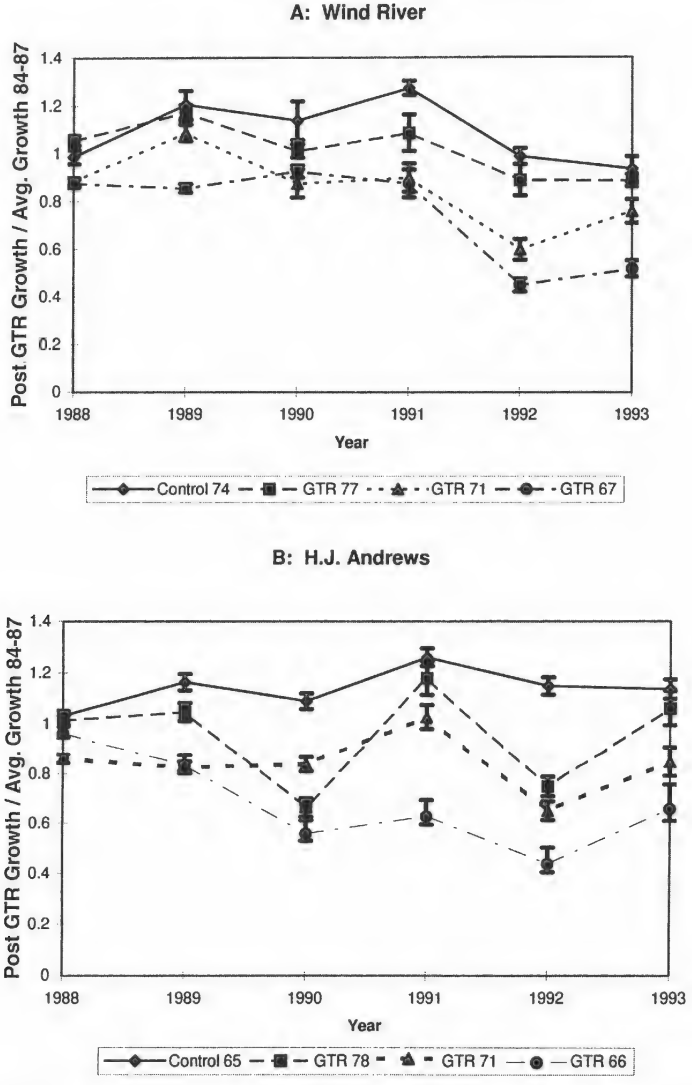

Figure 3. The change in basal area increment for each year of 1988-1993 divided by the average basal area increment for 1984-1987 at (A): Wind River and (B): H.J. Andrews. Each graph shows the control stand and three GTR stands. In the legend, the numbers following the stand type indicate the mean diameter at breast height (dbh). Graph values are the mean and standard error (shown with error bars) for 30 increment cores collected in each stand.

above the mean increment from 1983-1987. In contrast, the three GTR stands, with average retained tree diameters of 77, 71 and 67 centimeters (GTR 77, 71 and 67, respectively), have BAI changes which average 1.02, 0.85 and 0.75 of their mean increment from 1983-1987, respectively. In GTR 77 in 1988, 1989 and 1993, the overlap in standard error with the control indicates that there is not a statistically significant difference in BAI. All other GTR sample points are less than the control, and the three GTR stands average change in BAI is 13% less than their 1983-1987 average increment.

At the H.J. Andrews the control stand's annual BAI has increased 14% over the mean increment from 1983-1987. However, the three GTR stands with average diameters of 78, 71, and 66 centimeters, have changes in BAI of 0.95, 0.85 and 0.68 compared to their means from 1983-1987, respectively. The standard errors for GTR 78 and the control overlap in 1988, 1991 and 1993. All other GTR sample points are less than the control, and the three GTR stands average change in BAI is 17% less than their 1983-1987 average increment.

Discussion

The increasing use of green tree retention harvests has created an urgent need to understand the effects of this new harvest method on ecosystem processes. The intention of both dispersed and clumped green tree retention is to alter the nature of the timber harvest disturbance by retaining some of the original stand structure. Whether the impact of this altered disturbance regime achieves its objectives needs to be closely monitored. Many management objectives for GTR, such as speeding up recovery of habitat for late seral species or accelerating stand structural diversity can only be assessed with long-term and large-scale sampling and monitoring. In the interim, this study was designed to provide information about the early ecosystem response of a few stands to a GTR harvest.

The initial understory response on the study sites was a higher richness and evenness of species on the GTR than the forest or clearcut treatments. The GTR has more total species, a higher average number of species per plot and understory cover is more evenly distributed among species. However, while diversity measures are an important metric for comparing understories, a numerical index alone does not consider the functional role of individual species in seral development.

The understory study sites were sampled within 16 months after the harvest disturbance when invasive species peak in understory dominance (Franklin and Dyrness 1988; Halpern 1988). In 15-20 years after cutting, light levels are reduced as the regenerating forest creates a closed canopy. Residual shade-tolerant species from the pre-harvest stands which persist until canopy closure often begin to dominate the understory as shade-intolerant species die out. Most of the invasive species sampled in this study, which are shade intolerant, will not persist with seral development. The number and constancy of shade-tolerant species therefore provide some indication of the potential future understory diversity as light levels decrease with canopy closure. Furthermore, understories which presently have higher species evenness are less dominated by shade-intolerant, invasive species and therefore retain species which may survive the future reduced light levels of canopy closure. The longevity of shade-tolerant herbs during the stem exclusion stage (Oliver and Larson 1990) of forest development, however, has not been well studied, and in very low light conditions all herbaceous plants may die (e.g. under dense stands of shade-tolerant western hemlock foliage (Alaback 1982)).

At the time of sampling, the GTR and clearcut were dominated by invasive, shade-intolerant species creating a species composition distinct from the forest. The TWINSPAN classification of plots, however, also indicates that the composition of most GTR plots is distinct from the clearcut. The main difference in the GTR is the higher richness and evenness of species in each plot (Table 1), and the presence of more shade-tolerant species. For the species common to all three treatments, all of which are shade tolerant, constancy values are higher in the GTR than in the clearcut (Table 2). Four shade-tolerant species were only found in both the forest and GTR. Although there are many species common to the GTR and clearcut which were not found in the forest, species composition in GTR plots was more varied. Five of the GTR plots were classed with the forest plots in the first division of the TWINSPAN classification, while 23 GTR plots have a composition similar to clearcut plots in the final division.

Several hypotheses might explain the GTR's higher diversity and more variable plot-level species composition than the clearcut. The retention of trees on the harvest site may provide greater microsite variability than would be present in a clearcut. Logging disturbance may be more variable in a GTR because areas around the base of retained trees would have less yarding damage than the typical impact found in a clearcut. The partial retention of the overstory canopy may also affect understory microclimate, providing a mosaic of light and moisture conditions (Childs and Flint 1987; Hungerford and Babbitt 1987). The species unique to the GTR are associated with fairly dry (running club-moss) to very moist (rush), and shaded (wall lettuce) to full sunlight (black cottonwood) conditions (Klinka et al. 1989). The GTR, however, does not have two species, oak fern and Pacific trillium, which are sensitive to soil disturbance common with log yarding. Both plants were found only in the forest.

In the six GTR overstory retention stands there is a general decrease in basal area increment six years after harvest. This result was unexpected as studies in younger-age forests show basal area increment increases after trees are released from density-dependent competition (Worthington and Staebler 1961, Reukema 1975, Oliver and Larson 1990). Few studies, however, have examined the release response of mature trees which have been thinned to the low density common in green tree retention cuts. Newton and Cole (1987) found diameter growth continued to increase in two Douglas-fir stands of 120 and 140 year-old trees for 70 years after each was thinned in 1914 to about 75 dominant trees per hectare. Thinning research in 96 year-old Sitka spruce and western hemlock stands in southeast Alaska to about 300 trees per hectare, found diameter growth increased while unthinned stands showed decreasing diameter growth (Farr and Harris 1971). Old-growth Douglas-fir and western hemlock on the edge of a clearcut were found to have increased growth rates of 33% and 150% respectively, for a ten year period following the clearcut harvest (Chen et al. 1992). However, a study of the initial response of 70-150 year Douglas-fir with 60% removal found that the rate of diameter growth response decreased as the age of retained trees increased (Williamson and Price 1971). In mature and old-growth Douglas-fir stands where an average of 36% of the volume was removed, Isaac (1956) found a decline in diameter growth.

It is difficult to compare the response of GTR overstory trees with these studies because of variation in their retention densities, tree ages, species composition and location. The basal area increments for the control sites indicate growth has increased by 9 and 14% in adjacent uncut stands of the same age. Therefore it appears unlikely that climate conditions for growth during 1988 to 1993 were responsible for the GTR's decreased basal area increment. One hypothesis may be that the older trees sampled in this study may experience thinning shock (Oliver and Larson 1990) and initially respond by allocating more resources to below-ground growth. Size also appears to have some effect on response, as BAI in stands with larger average diameter did not decline as much as smaller diameter stands (Figure 3). The reasons for this pattern are not clear. Larger trees may be less stressed by changes in microclimate conditions which occur when the surrounding canopy is removed. Although a decrease in retained tree growth will not effect the "new forestry" objectives of increasing structural diversity and providing a source for large snags and logs, the unexpected result warrants further study.

The effects of new harvest techniques on retained overstory trees and the understory community will vary both with plant communities, geographic area, physiographic features and through time. Our results indicate an initial trend toward higher richness, evenness and number of shade-tolerant species, and reduced basal area growth in retained overstory trees following a green tree retention harvest. We suggest that further research is needed to investigate the effects of green tree retention, particularly:

- a permanent plot study of understory response, monitoring species composition before and after a green tree retention harvest
- monitoring of understory response through canopy closure
- a large-scale comparison of sites in the same plant association, including undisturbed old growth
- changes in overstory basal area increment over long post-harvest periods
- variation in overstory response with diameter, age, dominance, density and vigor of retained trees

Careful monitoring of harvest sites and broad-based, long-term studies are the only means of

assessing the full impact of green tree retention harvests on the forested ecosystems of the Pacific Northwest. We recognize, however, that policy makers and forest managers can not wait the several decades needed to get the results of these studies. In the meantime, we hope this study begins to provide information about the effects of these new management practices, until longer-term and more extensive monitoring of the effects of green tree retention harvesting can be completed.

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Geology of the Bungalow Pluton, Clearwater County, Idaho

Abstract

The Bungalow granite pluton is one of several relatively unstudied Eocene age (37-52 Ma) plutons located within the Clearwater igneous province of northern Idaho. This province lies along the Kelly Forks fault, a major northwest-trending strike-slip structure that separates the Cretaceous age (60-90 Ma) Idaho batholith from Proterozoic (850-1400 Ma) metamorphic rocks. This study used geologic mapping, together with whole rock geochemical analyses and petrographic thin section observations, to document the internal chemical, petrographic and structural characteristics of the pluton and to reconstruct the crystallization behavior and mode of emplacement. The pluton forms a 225 km^2 by 1600 m exposure of granite with steep, unaltered and undeformed margins and a well defined negative gravity anomaly. The west half of the pluton has an upper surface of porphyritic granite. The large NW -trending Kelly Forks fault and 3 N-S striking normal faults cut the pluton. These new observations, interpreted in context of previous limited radiometric age dating and structural analysis of the Kelly Forks fault, suggest that the pluton is an isolated body passively emplaced along a strike-slip tectonic setting which was active during the Paleogene. This setting contrasts with the northeast-trending normal faults associated with Eocene igneous provinces adjacent to the southern part of the Idaho batholith. The pluton is composed of a suite of texturally diverse (fine-grained to porphyritic), yet remarkably homogeneous high-silica (75-77 wt % SiO_2), metaluminous, biotite granite. The preferential occurrence of porphyritic textures and hydrous minerals near the edges of the pluton suggest that the pluton crystallized from the margins inward with no significant differentiation. In addition, the pluton was intruded by minor occurrences of rhyolite porphyry dikes, quartz syenite, lamprophyre dikes and has subsequently undergone limited, post magmatic hydrothermal alteration.

Introduction

Ongoing geologic studies adjacent to the Cretaceous Idaho batholith located in northern and central Idaho have documented numerous Eocene intrusive and volcanic provinces (Lewis et al., 1992a, 1992b; Lewis and Kiilsgaard, 1991; Reynolds, 1991; Lewis, 1990; Motzer, 1985; Simpson, 1985; Bennett and Knowles, 1983; Hardyman, 1981; Nold, 1968; Hietanen, 1963). These provinces have been interpreted by most previous researchers to represent post-orogenic igneous activity following the subduction-related generation of the Idaho batholith. Many of these Eocene plutons have been mapped and sampled on reconnaissance scale, but little has been done to document in detail their internal petrographic and geochemical variability or to establish the structural controls on emplacement and post magmatic deformation.

This paper presents new field and geochemical information to document the internal petrologic and structural character of the Bungalow pluton, one of a series of chemically diverse Eocene intrusions and volcanic centers that make up the Clearwater igneous province of northern Idaho. The data suggest that this high-silica pluton is surprisingly homogeneous and developed by inward crystallization. The pluton has also been intruded by later dikes and undergone late stage hydrothermal alteration resulting in mineral assemblages and geochemical anomalies not observed in other Eocene plutons surrounding the Idaho batholith. Structural observations indicate that igneous activity associated with the Clearwater igneous province, and the Bungalow pluton in particular, is closely confined to a northwest-trending strike-slip fault system that was active during the Paleogene (Ewing, 1980). This tectonic setting is in contrast to northeast-trending extensional faults associated with Eocene igneous provinces adjacent to the Atlanta lobe of the Idaho batholith (Bennett, 1986; Motzer, 1985).

Field Relations

Geologic Setting

The Bungalow pluton intrudes the northern margin of the Bitterroot lobe of the Idaho batholith and Proterozoic metasediments of the Belt Supergroup (Fig. 1). It is dissected by the North Fork of the Clearwater River, providing 1600 m of vertical exposure. The pluton lies adjacent to and is partly cut by the Kelly Forks fault, one of several large northwest trending fault zones that transect northern Idaho. The fault forms a km-wide zone of deformation that separates the older

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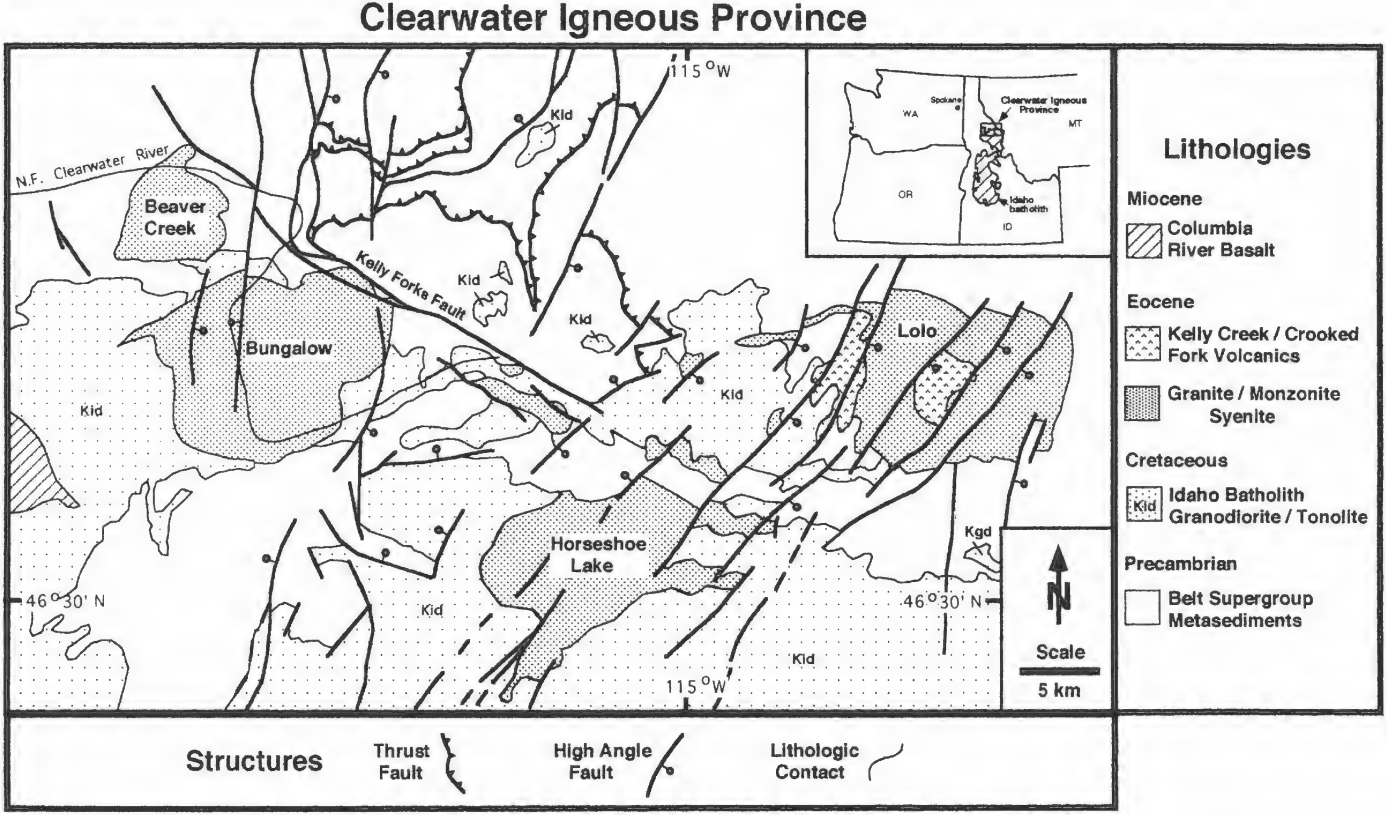

Figure 1. Simplified geologic map of the Clearwater igneous province highlighting Eocene intrusions and major structural features (compiled from Lewis et al, 1992a, 1992b; Reynolds, 1991; Bennett, 1986).

igneous and metamorphic country rocks. An array of Eocene plutons that compose the Clearwater igneous province have intruded along the fault zone (Fig. 1). Childs (1983) has provided evidence that alternating episodes of kilometer-scale right- and left-lateral strike-slip movement have occurred along the fault during the Paleogene. However, offset of the Bungalow pluton by the Kelly Forks fault is minimal, with latest movement consisting of right-lateral oblique-slip movement. North of the Kelly Forks fault, Belt Supergroup metasediments are complexly folded and thrust faulted. South of the fault, large expanses of Cretaceous tonalite and granodiorite, together with lesser amounts of Precambrian metamorphic rock, are exposed. A series of steep-dipping, northeast-trending faults cut the plutonic rocks and truncate the southeast end of the Kelly Forks fault. Other Eocene plutons located within the Clearwater igneous province and along the northwest trend of the Kelly Forks fault include the Beaver Creek stock, the Horseshoe Lake pluton, the Lolo Hot Springs pluton, and numerous unnamed bodies of syenite (Fig. 1; Lewis et al., 1992a). Rhyolite dikes are generally abundant throughout the Clearwater igneous province and intrude all the plutons (Lewis et al., 1992a).

Potassium/argon age determinations on biotite, 45 +/- 2.0 Ma, (Armstrong, et al., 1977) and 43.1 +/- 1.4 Ma (Hietanen, 1969), provide the only available age constraints for the Bungalow pluton. Owing to the overall medium to coarse-grained texture of the pluton, which suggests slow cooling and extensive subsolidus recrystallization, the ages could be anomalously young, reflecting cooling ages rather than crystallization ages. Clearly, age determinations of fine-grained granite and crosscutting dikes are needed. Nevertheless, the available age data contrast with the late Cretaceous ages (65-90 Ma) assigned to plutons of the Bitterroot lobe of the Idaho batholith and are remarkably similar to numerous other Eocene plutons in the region which span an age range of 38-50 Ma (Armstrong, 1974).

Form of Intrusion

The Bungalow pluton forms a continuously exposed body approximately 15 km in diameter and 1600 m thick (Fig. 2). The floor is not exposed. Contacts between the pluton and country rock are steep-dipping and abrupt. No evidence of xenoliths or flow foliation occur in the granite nor has there been any appreciable contact metamorphism or hydrothermal alteration of the adjacent country rock. This is in contrast to other more mafic Eocene plutons adjacent to the Idaho batholith, such as the Beaver Creek stock, which show well defined igneous foliation and abundant xenoliths.

Reconnaissance gravity survey data indicate the existence of a large, well-defined negative gravity anomaly centered over the pluton and supports field observations that the pluton is steep-sided and upright (Zeitz et al., 1978). Moreover, the negative gravity anomaly, together with the absence of a distinct magnetic anomaly, suggest that the pluton has no mafic root; the pluton is therefore an isolated igneous body.

The west half of the pluton is topographically subdued. Irregular sheets of porphyritic granite are exposed over much of this area. Porphyritic granite is partly surrounded by fine-grained granite and grades downward into medium- and coarse-grained granite. Vertical exposures of porphyritic granite range from 100 to 400 m.

Rhyolite porphyry dikes intrude the margins and interior of the pluton and surrounding country rock in numerous locations (Fig. 2). The dikes form narrow, resistant, steeply dipping ridges that can be traced for hundreds of meters to over 12 km, and range in width from 3 to 30 m. In addition, a northeast-trending swarm of rhyolite dikes occurs near the southeastern margin of the pluton (Fig. 2; Lewis et al., 1992a).

A few lamprophyre dikes are exposed within and around the pluton. They occur as dark, solitary, near-vertical dikes 1 to 3 m wide exposed for hundreds of meters along strike. At some contacts, the adjacent granite has been baked and altered, indicating that the dikes were emplaced at high temperature into solidified granite. In no cases are the dikes observed to be in a state of disaggregation or partial assimilation. The occurrence of crosscutting, undeformed lamprophyre dikes, the first to be documented in the Eocene plutons surrounding the Idaho batholith, provides a significant contrast to the older (Cretaceous), deformed and comingled, synplutonic, mafic dikes within the plutons of the Idaho batholith (Hyndman and Foster, 1988).

A small (1 km^2) pod of altered quartz syenite is located within the porphyritic granite section of the Bungalow pluton. Its vertical exposure is

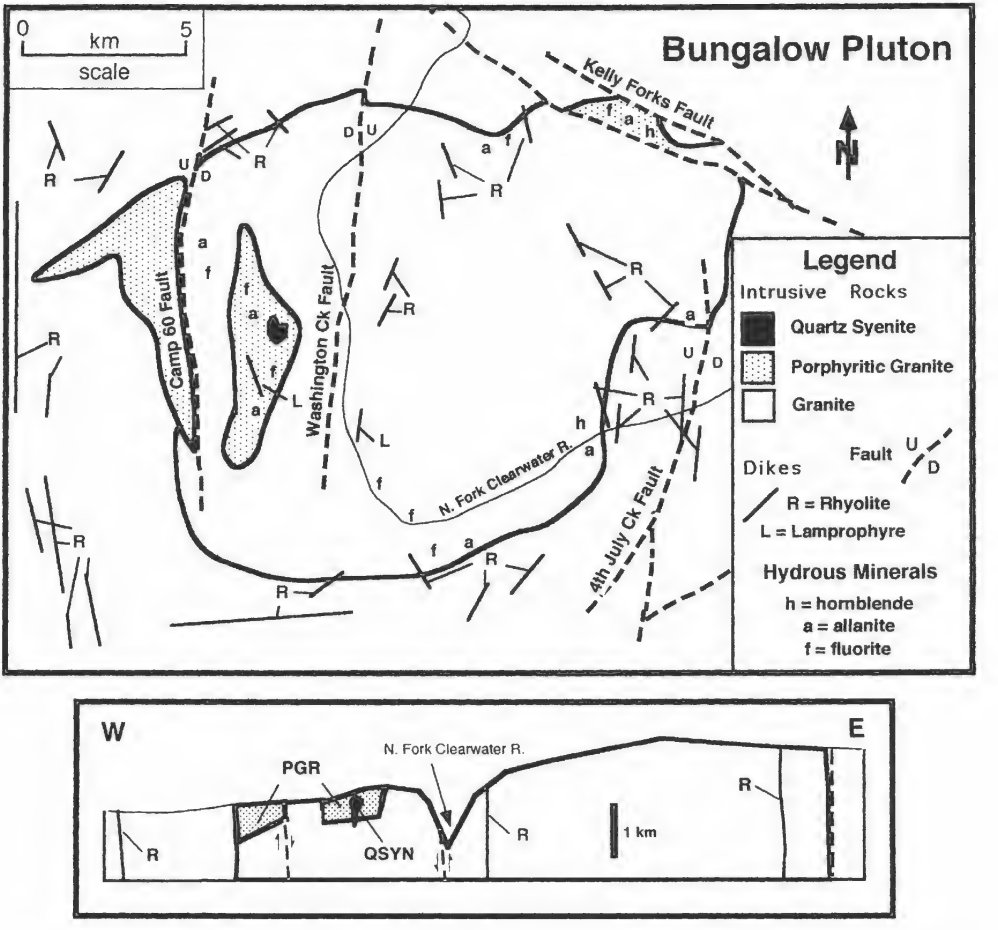

Figure 2. Geologic map and interpretative W-E cross section of the Bungalow pluton showing major rock types, cross cutting faults and dikes and the distribution of hydrous minerals compiled from Lewis et al, 1992a; Reynolds, 1991; Hietanen, 1963).

200 m. A 3 m wide fine-grained margin marks the northern contact with porphyritic granite, whereas the interior is coarse grained. An abundance of fractured mineral grains and cloudy feldspar indicate that hydrothermal alteration was focused on the quartz syenite. More extensive outcrops of syenite have been mapped in the region outside of the complex as separate intrusions (Fig. 1; Lewis et al., 1992a).

Greisenized granite forms groups of vertical veins and subhorizontal lenses in the southwestern quarter of the pluton. Veins and lenses vary in size from 0.5 to 2 m thick by 1 to 5 m long and are sharply discordant with the wall rock. The veins show no preferred orientation and appear to have developed independently of the well-developed north-trending joint pattern in the granite.

The pluton is deformed by three north-trending high angle normal faults. Evidence for these faults is abundant in the northern part of the pluton, but becomes more obscure to the south perhaps indicative of greater fault displacement to the north. The most prominent fault is the Washington Creek fault that splits the pluton roughly

in half (Fig. 2). The west half of the pluton is the down thrown block with a possible displacement of 100 to 700 m. Two other faults bound the east and west margins of the pluton. The western-most fault, exposed at Camp 60, together with the Washington creek fault, separate a down-dropped block of porphyritic granite from an uplifted eastern block of coarse-grained granite. On the extreme east side of the pluton a large north-trending fault is well exposed at Fourth of July creek. This fault offsets Cretaceous igneous rocks, as well as rhyolite dikes with the east block down-dropped. All of the north and northeast-trending faults in the region postdate the Kelly Forks fault, yet predate the extrusion of Columbia River basalt (Lewis et al, 1992a).

Petrography

The granitoid rocks within the pluton are divided by grain size and texture. Thin section point counts of 1000 points per sample were used to derive the normalized modal mineral distribution for the three major phases (Table 1 and Fig. 3) and to determine the type and amount of accessory minerals present. The bulk of the pluton is composed of light-gray, fine-, medium- and coarse-grained, subsolvus biotite granite. Representative samples are hypidiomorphic equigranular and contain subequal proportions of perthitic orthoclase, plagioclase and quartz. The dominant mafic mineral is brown biotite which occurs throughout the pluton in modal amounts of 1-5 %. Trace amounts of allanite, apatite, zircon and magnetite are also present. Rare occurrences of fluorite and extensively-replaced hornblende are found near the margins of the pluton, whereas biotite is distributed equally throughout the pluton. Porphyritic granite occurs over large parts of the western half of the pluton and is composed of large euhedral phenocrysts of orthoclase and quartz set in a fine-grained to granophyric groundmass.

Rhyolite dikes consist of a blue-gray groundmass in which euhedral pink orthoclase, white plagioclase, and bipyramidal smoky quartz phenocrysts are embedded. Phenocryst contents range from 17-51 modal %. Accessory biotite is present along with trace amounts of pyroxene, amphibole, apatite, zircon, magnetite, and fluorite. Millimeter-scale flow-banding is present in some rhyolite dikes. Banding occurs as dark-gray layers of obsidian and quartz-feldspar spherulites that

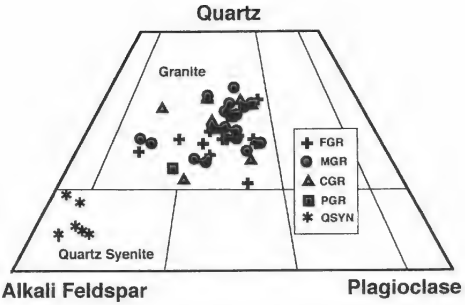

Figure 3. Modal distribution of plutonic rocks associated with the Bungalow pluton. Modes were determined by petrographic thin section point counting (see also Table 1). Symbols: FGR = fine-grained granite, MGR = medium-grained granite, CGR = coarse-grained granite, PGR = porphyritic granite, QSYN = quartz syenite.

are separated by a pale white, fine-grained matrix of plagioclase, K-feldspar and quartz. Banding roughly parallels the walls of the dikes and is commonly convoluted.

Yellow-brown to dark-gray lamprophyre dikes consist of a sparsely porphyritic, intergranular arrangement of battlemented biotite laths (26-49 modal %), together with subequal amounts of plagioclase, potassium feldspar, and augite. Large (1-3 cm) isolated crystals of pink orthoclase are the only visible phenocrysts. Small (1-3 mm) vug-like cavities lined with quartz and calcite are abundant in some of the lamprophyres.

The mineralogy of the quartz syenite includes milky-white perthitic alkali feldspar, albite, and dark green clots of aegirine-augite. Much of the alkali feldspar exhibits a checkerboard pattern, indicative of pervasive albitic alteration (Parsons and Brown, 1984). The larger plagioclase phenocrysts are strained and cracked from post-crystallization deformation. In addition, a very-fine-grained acicular blue amphibole, possibly arfvedsonite or riebeckite, partly replaces pyroxene. Accessory minerals include siderite and specular hematite. Fluorite and topaz are present in trace amounts. Although small in size, the sodium-rich quartz syenite is the first to be described from Eocene granites adjacent to the Idaho batholith. Other Eocene syenites described thus far from the Clearwater igneous province are not hydrothermally altered.

TABLE 1. Normalized modal point counts of 46 granite thin sections vs elevation and distance from pluton margin

Sample	Elevation	Distance	Texture	Quartz	K-spar	Plag	Biotite	h	f	a	ap	mia
203	1591	0.1	APL	34	31	35	G					
35	1070	1.4	APL	43	33	23	G4		X	X	X	
120	1246	4.6	APL	22	35	43	BG2					
368	914	0.7	APL	30	31	39	B7		X	X	X	
67	1366	0.3	FGR	33	35	32	GM3			X		
193	2048	2.8	FGR	33	28	39	BMG					F
192	2060	2.8	FGR	34	32	34	B6					F
364	1905	2.4	FGR	27	42	31	BG3					
340	1768	1.2	FGR	41	26	33	B6		X			
462	786	0.1	FGR	39	30	31	G3					
289	1524	0.8	FGR	35	31	34	BMG5				X	
259	1271	4.3	FGR	42	24	34	G1					
14	780	0.1	FGR	43	26	31	BM3					
301	1524	0.4	FGR	28	44	72	G2		X			F
355	649	6.5	FGR	39	30	31	BG3					F
327	1753	2.7	MGR	39	29	32	BM4					
27	646	4.0	MGR	38	35	27	BG4					A
34	671	4.5	MGR	36	35	29	G2		X			
59	671	4.8	MGR	42	24	34	BMG4		X			
105	1341	2.7	MGR	39	30	31	B4					
329	1737	2.2	MGR	33	32	35	BMG4					
22	702	1.2	MGR	28	31	41	BMG4		X			F
291	1561	0.2	MGR	33	34	33	B6	1		X	X	
175	646	4.5	MGR	32	28	40	B5			X	X	
243	786	0.1	MGR	35	37	28	B5			X	X	
302	1524	0.7	MGR	32	52	16	G3	1	X	X	X	A
305	1412	1.1	MGR	32	27	41	G6					F
363	1981	1.9	MGR	40	31	29	BM3					
258	1545	6.5	MGR	33	32	35	GM4		X			
244	738	1.0	MGR	36	36	28	B3		X			
245	732	1.5	MGR	36	36	28	BM3					
90	1158	3.4	MGR	29	40	31	B5		X	X	X	
261	1049	3.4	MGR	36	33	31	B5		X			
13	1073	0.8	CGR	23	49	28	B7					
4	610	0.5	CGR	44	33	23	B6		X	X	X	
10	1091	2.7	CGR	41	45	14	B7			X	X	
283	704	1.0	CGR	46	26	28	B6			X		
184	1597	0.6	CGR	30	56	14	GM6	X		X		A
403	610	1.4	CGR	44	33	23	B5		X	X		
296	1524	0.8	CGR	33	54	13	BG3		X	X		
81	1052	2.0	CGR	32	40	28	B4		X	X	X	
456	631	3.2	CGR	26	50	24	B3					
109	1329	3.5	PGR	33	45	22	B5			X		A
110	1311	3.4	PGR	43	22	35	B10		X	X	X	
373	1146	7.5	PGR	42	29	29	B5		X	X		

key to headings and symbols for hydrous minerals:

Biotite: B = brown biotite; G = green biotite; M = muscovite; numbers = modal percent

h = hornblende, numbers = modal percent; f = fluorite, a = allanite, ap =apatite,

x = presence in sample; mia = occurence of miarolitic cavities, F = few, A= abundant

The greisens within the pluton consist of a vein-controlled hydrothermal alteration mineral assemblage dominated by quartz (60-80 modal %) and muscovite (20-40 modal %) with accessory cassiterite and specular hematite and trace fluorite and topaz. Quartz has recrystallized into small anhedral grains that exhibit undulatory extinction and sutured grain boundaries. Muscovite has replaced nearly all of the feldspar and biotite. Cassiterite is disseminated throughout the greisens as 0.05-0.3 mm euhedral hexagons, whereas topaz forms isolated, octagonal grains rimmed by muscovite.

Geochemistry

Thirty eight representative samples of the pluton were analyzed, including granite (22 samples), rhyolite, quartz syenite and hydrothermally altered rocks. Two blind duplicates were analyzed with each set of samples. Chemex Laboratory Inc. performed the whole-rock determinations of 11 major element oxides. 1-2 kg hand samples were submitted to multiple stage crushing and pulverizing to -150 mesh in a zirconia ring. After pulverizing, 20 gram sub-samples were selected, fused and then analyzed by inductively coupled plasma-atomic emission spectroscopy (ICP-AES). Detection limits were 0.01 wt % for each oxide. Ferrous iron content was determined separately by acid decomposition-titration. Major element oxides were reproducible to less than 5 wt % (except TiO_2 and P_2O_5). Bondar-Clegg Inc. performed the minor and trace element analyses on each of the granites. These samples were prepared in a manner similar to the whole-rock sample preparation methods and analyses were obtained by instrumental neutron activation analysis (INAA). Trace elements were reproducible to less than 15 % (except Yb). The analytical results, together with standard deviations and duplicate analyses are compiled in Table 2.

Major Elements

The major element oxide abundances for the granite are remarkably homogeneous (Table 2). The granites are high-silica (75-77 wt %) and metaluminous to weakly peraluminous (Fig. 4). MgO and CaO show a reciprocal relationship as SiO_2 increases (Fig. 5). Trends for K_2O and Na_2O are poorly developed and may be affected by deuteric alteration. The major element compositions of the rhyolite porphyry dikes are very similar to the granite (Table 2). The hydrothermal alteration has affected some of the apical parts of the pluton and masks some of the chemical characteristics of the granitic rocks. For example, the quartz syenite is complicated by an overprint of sodium enrichment indicative of albitic alteration (Table 2).

Trace Elements

Compositional variations for most of the trace elements in granite are not significant (Table 2 and Fig. 5). Barium however, decreases with increasing silica, and chondrite-normalized rare earth elements (REE) decrease with increasing atomic number (Fig. 6). All granites show a pronounced negative Eu anomaly, with porphyritic granite having the smallest Eu anomaly. The albitized quartz syenite is enriched in Ba and light REE and depleted in Rb and heavy REE relative to granite (Table 2). Greisens contain elevated amounts of Cs, Rb, Th and U (Table 2) as well anomalous Sn, Mo, W, Nb, and Ag values (Reynolds, 1991).

Volatiles

Little information is available to help constrain the volatile content of the magma. The only hydrous mineral present in accessory amounts is biotite (Table 1). Rare hornblende (extensively replaced by biotite) and trace amounts of apatite and topaz are present and concentrated in the marginal regions of the pluton (Table 1, Fig. 2) where water was presumed to be more abundant. In addition, the chlorine content of biotite is highest in samples taken from porphyritic granite near the projected roof of the pluton (Reynolds, 1991). Small (0.5-1 cm) miarolitic cavities are observed in 26 % of the hand specimens and thin sections (Table 1). The miarolitic cavities are abundant throughout the pluton and become larger with increasing elevation and towards the margins of the pluton. The cavities provide evidence that water exsolved in the late stages of crystallization.

Discussion

Emplacement

The emplacement and subsequent deformation of the Bungalow pluton appear to have been controlled primarily by the Kelly Forks fault and a

TABLE 2. Major and trace element whole rock analyses for the Bungalow pluton and associated rocks.

*Major element oxides (wt %)

	FGR Avg	(n=6) Stdev	MGR Avg	(n=10) Stdev	CGR Avg	(n=4) Stdev	PGR Avg	(n=2) Stdev	RHY Avg	(n=8) Stdev	LAM Avg	(n=2) Stdev	QSYN Avg	(n=4) Stdev	GREI Avg	(n=2) Stdev
SiO_2	76.88	0.41	77.02	0.90	76.13	0.64	74.89	0.49	76.54	0.92	56.21	0.66	70.22	0.06	78.43	4.16
TIO_2	0.04	0.02	0.06	0.04	0.12	0.05	0.20	0.08	0.15	0.06	1.61	0.23	0.20	1.03	0.06	0.01
AL_2O_3	12.85	0.28	12.59	0.37	12.79	0.23	13.36	0.07	12.70	0.45	16.50	0.24	15.38	1.05	12.62	2.48
FEO	0.81	0.16	0.86	0.14	1.01	0.09	1.40	0.33	0.78	0.34	5.24	1.70	1.18	0.75	2.43	0.25
FE_2O_3	0.16	0.08	0.25	0.16	0.44	0.13	0.24	0.15	0.63	0.28	2.29	1.61	1.14	0.01	1.76	0.84
MnO	0.03	0.02	0.03	0.01	0.02	0.01	0.03	0.01	0.02	0.01	0.13	0.02	0.03	0.10	0.12	0.12
MGO	0.35	0.22	0.07	0.04	0.18	0.09	0.29	0.03	0.11	0.07	3.04	0.05	0.28	0.23	0.11	0.06
CAO	0.06	0.03	0.52	0.32	0.77	0.53	1.09	0.08	0.65	0.23	5.52	0.21	1.02	2.22	0.20	0.08
NA_2O	4.14	0.31	3.97	0.35	3.66	0.21	3.58	0.01	3.70	0.31	5.21	0.15	7.11	1.94	0.21	0.01
K_2O	4.60	0.37	4.47	0.57	4.85	0.26	4.87	0.01	4.70	0.27	3.84	0.95	3.40	0.03	4.01	0.85
P_2O_5	0.07	0.06	0.06	0.04	0.06	0.04	0.08	0.06	0.05	0.04	0.48	0.06	0.04	0.04	0.02	0.01
Trace Elements (ppm)																
Cs	6	4	7	2	4	3	4	1	3	1	1	0	13	12	8	14
Rb	349	180	216	33	164	47	160	85	209	64	124	56	616	50	192	91
Th	24.1	2.8	20.4	5.2	17.4	3.7	17.4	7.6	20.7	4.9	23.1	0.6	34.9	1.7	13.1	7.3
U	6.8	2.7	5.2	1.7	4.2	1.5	4.2	1.3	5.3	2.0	3.9	1.0	9.2	1.1	3.7	1.7
Ta	5.1	4.7	2.2	1.0	1.1	0.7	1.0	0.6	1.6	0.8	1.4	0.4	4.4	1.6	1.2	0.5
Ba	42	12	74	41	180	67	340	14	143	175	698	198	25	0	450	551
Hf	6	2	4	1	5	2	5	1	5	2	6	1	3	1	4	2
La	12	5	21	13	43	8	43	23	34	17	63	27	13	1	29	13
Ce	25	8	35	19	71	11	69	15	65	27	108	18	27	3	51	19
Sm	3.7	1.5	4.5	1.4	6.0	1.0	5.8	1.4	6.6	1.9	10.4	2.1	6.0	0.2	5.8	2.2
Eu	0.2	0.2	0.2	0.1	0.3	0.2	0.5	0.0	0.4	0.2	0.5	0.0	0.5	0.0	0.3	0.2
Tb	0.9	0.5	1.2	0.3	0.9	0.5	0.7	0.5	1.4	0.3	1.3	0.2	1.7	0.4	1.1	0.4
Yb	4.16	1.84	5.08	1.89	2.76	1.97	1.95	0.08	3.80	1.59	2.25	0.50	3.50	0.71	3.11	1.49
Lu	0.65	0.34	0.88	0.29	0.47	0.33	0.38	0.04	0.67	0.20	0.45	0.06	0.65	0.07	0.50	0.23

*whole rock values are normalized to 100 % water free n = sample population

Rock Type abbreviations:

FGR = fine-grained granite; MGR = medium-grained granite; CGR = coarse-grained granite; PGR = porphyritic granite

LAM = lamprophyre dikes; QSYN = quartz syenite; GREI = gresien

TABLE 2. (Con't)

Duplicate analyses (normalized to 100 % water free)

Sample #	30	30-D	% Dif	455	455-D	% Dif
SiO_2	74.59	74.61	0.0	76.18	76.44	0.3
TIO_2	0.23	0.20	14.0	0.02	0.02	0.1
AL_2O_3	13.69	13.62	0.5	13.21	13.02	1.5
FEO	1.46	1.53	4.7	0.56	0.55	1.8
FE_2O_3	0.56	0.52	7.6	0.23	0.23	0.1
MnO	0.03	0.03	0.1	0.05	0.05	0.1
MGO	0.03	0.03	0.1	0.07	0.07	0.1
CAO	0.66	0.63	4.8	0.46	0.48	4.4
NA_2O	3.99	4.02	0.9	4.38	4.33	1.1
K_2O	4.71	4.78	1.4	4.83	4.79	0.8
P_2O_5	0.04	0.02	66.7	0.01	0.01	0.1

							Bondar-Clegg standards		
Sample #	30	30-D	% Dif	455	455-D	% Dif	GS89-2	GS89-2D	% Dif
Cs	3	3	0.0	47	47	0.0	0.8	0.8	0.0
Rb	190	190	0.0	583	573	1.7	40	46	14.0
Th	18.0	20.0	10.5	27.7	27.8	0.4	3.5	3.1	12.1
U	4.5	4.9	8.5	7.8	7.9	1.3	1.4	1.4	0.0
Ta	1.2	1.4	12.5	8.5	8.4	1.2	0.30	0.30	0.0
Ba	510	560	9.3	25	25	0.0	510	540	5.7
Hf	7	8	9.2	5	6	18.2	3	3	0.0
La	53	59	10.7	9	10	10.5	10	10	0.0
Ce	110	125	12.8	17	20	16.2	24	23	4.3
Sm	8.1	8.4	3.6	5.8	5.6	3.5	1.0	1.0	0.0
Eu	0.5	0.5	0.0	0.5	0.5	0.0	0.5	0.5	0.0
Tb	1.1	1.2	8.7	1.4	1.4	0.0	0.9	0.8	11.8
Yb	1.5	3.0	66.7	4.0	4.0	0.0	3.0	3.0	0.0
Lu	0.5	0.5	0.0	0.6	0.8	28.6	0.5	0.5	0.0

Major element oxide analyses by Chemex Laboratory using ICP-AES: order #I-9024034, I9013506
Trace element analyses by Bondar-Clegg using INAA: order # R90-10599, R90-12499
% Dif = percent difference; A "D" at the end of a sample number indicates duplicate analysis

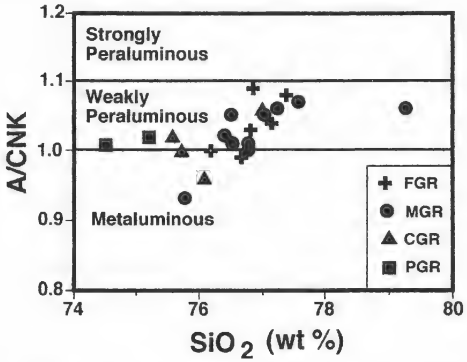

Figure 4. Plot of molecular Al_2O_3 / CaO + Na_2O + K_2O (A/CNK) vs. SiO_2 for granites of the Bungalow pluton. Samples straddle the alumina saturation divide (A/CNK = 1.0) and show a subtle trend towards an increasing peraluminous character with increasing silica content. Symbol abbreviations are the same as in Fig. 3. Divisions in alumina saturation are from Ragland (1989).

few north-trending normal faults. Activation of N-W trending strike slip faults, concomitant with clockwise rotation, has been documented to have occurred in the Pacific Northwest during the Paleogene (Ewing, 1980). The Kelly Forks fault in particular is a local expression of this northwest-trending regional structure (Childs, 1983). This tectonic setting could have created NE-SW shear-induced extensional stress which facilitated emplacement. This type of extension contrasts with the NW-SE tensional basin and range type of extension found in the Challis (Bennett, 1986) and Selway-Bitterroot (Motzer, 1985) areas of central Idaho.

Reconnaissance geophysical evidence (Zeitz et al., 1978) suggests that the pluton lacks a large mafic root; it is therefore likely to be an isolated body and not the cupola of a large batholith. The lack of interaction with country rock and narrow fault margins suggest that magma ascended by

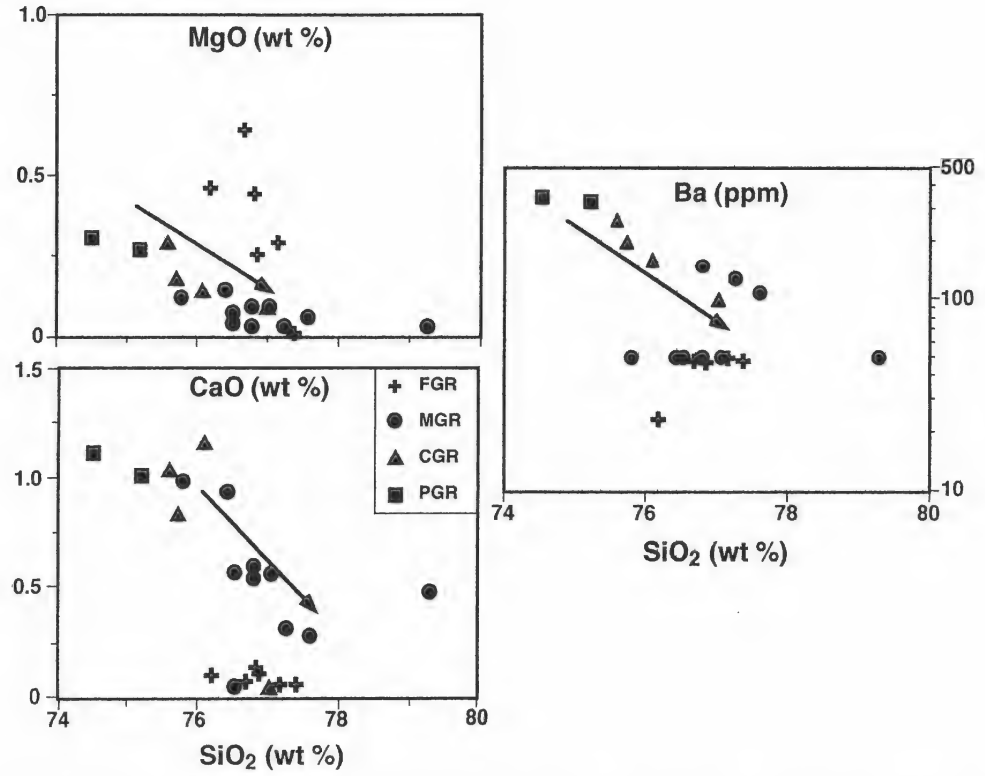

Figure 5. Representative silica covariation diagrams for the Bungalow pluton. Arrows indicate interpreted trends in selected oxides/elements verses silica. Plotted data are normalized to 100 % water free. Symbol abbreviations are the same as in Fig. 3.

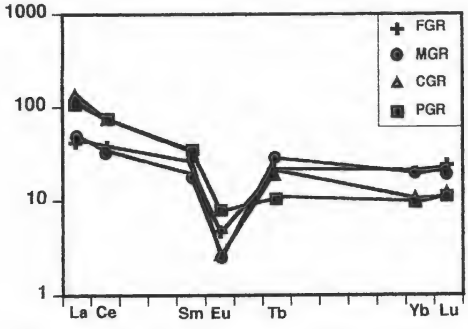

Figure 6. Chondrite normalized REE plots for the Bungalow pluton. Values shown are averages for each rock type. All rock types show a pronounced negative Eu anomaly. REE elements that were not analyzed are interpolated between the nearest analyzed neighbor elements. Symbol abbreviations are the same as in Fig. 3.

shouldering aside country rock along weak zones, rather than by forceful stoping or assimilation of the country rock. The abundance of porphyritic granite, hydrous minerals, miarolitic cavities and rhyolite porphyry dikes in the down-dropped west half of the pluton suggests that this area was close to the original roof of the pluton. Similar down-dropped blocks of foundered porphyritic roof are observed in the Challis igneous province of central Idaho (Hardyman, 1981) and in the nearby Lolo Hot Springs pluton (Fig. 1 and Nold, 1968).

Crystallization

The pluton is remarkably homogeneous in its granitic composition and appears to have crystallized from the margins of the intrusion inward. The spatial position of trace hydrous phases as well as fine-grained and porphyritic granitic

textures decrease systematically inward towards the center of the pluton, suggesting that water contents and thermal contrast were larger near the margin of the pluton. In addition, the elevated position of the porphyritic granite within the pluton suggests that it was the first to solidify as the pluton cooled.

Minor and trace element patterns provide some evidence of the crystallization pattern within the pluton. Barium, for example, decreases with increasing SiO_2 and reflects its selective incorporation into biotite and K-feldspar (Fig. 5). The pronounced light REE depletion (Fig. 6) can be attributed to the late crystallization of allanite and the negative Eu anomaly suggests that the magma was derived from a plagioclase-bearing source.

The quartz syenite bears some geochemical and spatial similarities with the porphyritic granite, but is complicated by an overprint of albitic alteration. The fine-grained margin of the quartz syenite suggests that it was emplaced after the granite had solidified, rather than developing comagmatically with the porphyritic granite. Alternatively, the margin may represent a fine-grained facies of pervasive albitic alteration resulting from second boiling of volatiles. Supporting field and petrographic evidence for this is manifest in the pervasive albitic replacement of K-feldspar and abundant fracturing of quartz and plagioclase.

The development of the quartz-muscovite greisens is also related to the concentration of magmatic fluids late in the crystallization history of the pluton. Excess magmatic pressures which can develop as a result of a vapor phase volume increase during late stage magma crystallization may have cracked the carapace of the intrusion in several places. The resulting cracks may have been invaded by acidic fluids resulting in alteration of the feldspars and biotite to produce muscovite and quartz. In addition, some of the metals (Sn, W in particular) accompanied the rising fluids.

The geochemical signature of the rhyolite porphyry dikes is very similar to the granite (Table 2). Moreover, the field occurrence of rhyolite dikes closely coincides with the margins of the pluton (Fig. 2). Because the dikes do not intrude nearby Columbia River basalt and the dikes are not commonly located in areas far from the occurrence of Eocene intrusions, the rhyolite dikes are broadly constrained in age to between middle Miocene (17 Ma) and late Cretaceous (66 Ma). Elsewhere, surrounding the batholith, rhyolite dikes occur in similar spatial and chemical relationship with Eocene granites (Lewis et al., 1992a; Bennett, 1986; Motzer, 1985; Leonard and Marvin, 1982). Several of these rhyolite dikes have been dated and all coincide closely (± 2 my) with the time span of Eocene igneous activity in the respective areas (Marvin et al., 1989; Armstrong, 1975). Although a close spatial coincidence and chemical similarity exist between the pluton and the dikes, confirmation of a comagmatic and coeval relationship will require radiometric dating of the dikes.

Summary

The Bungalow granite pluton is important because it is one of several relatively unstudied Eocene plutons located within the Clearwater igneous province of northern Idaho that intruded along the Kelly Forks fault, a major northwest-trending strike slip structure. The pluton is a remarkably homogeneous body of texturally diverse, high-silica, biotite granite. The variation in the geochemistry of the pluton is minimal for most major and trace elements over 1.6 km of vertical relief and 225 km^2 of horizontal exposure. The occurrence of porphyritic textures and hydrous minerals near the margins of the pluton suggest that magma may have crystallized inward. Later subordinate rhyolite porphyry and lamprophyre dikes and a pod of quartz syenite intrude the granite. Minor post-magmatic hydrothermal alteration is confined to the upper part of the pluton and is preserved as albitic and greisenized mineral assemblages.

The pluton is a fault-bounded, steep-sided body with unaltered margins and a well defined negative gravity anomaly. The west half of the pluton has an upper surface of porphyritic granite that may represent the roof of the pluton preserved, in part, due to down dropping along N-S normal faults that post date the intrusion. These observations, when considered in context of other radiometric and structural data, suggest that the pluton is an isolated body passively emplaced in a tectonic setting which produced tensional shearing along the Kelly Forks fault as a result of strike-slip movement and clockwise rotation during the Paleogene. This tectonic setting contrasts with the northeast-trending normal faults associated with Eocene igneous provinces adjacent to the southern part of the Idaho batholith.

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Geologic Sources of Asbestos in Seattle's Tolt Reservoir

Abstract

Water from Seattle's South Fork Tolt Reservoir contains chrysotile and amphibole asbestos fibers, derived from natural sources. Using optical petrographic techniques, X-ray diffraction, and scanning electron microscopy, we identified the geologic source of these asbestiform minerals within the watershed. No asbestos was found in the bedrock underlying the watershed, while both chrysotile and amphibole fibers were found in sediments transported by Puget-lobe glacial processes. These materials, widely distributed throughout the lower watershed, would be difficult to separate from the reservoir sediments. The probable source of this asbestos is in pods of ultramafic rock occurring north of the watershed. Because asbestos is contained in widespread Puget-lobe glacial materials, it may be naturally distributed in other watersheds in the Puget Sound area.

Introduction

Located in the Cascade Mountains of Washington, about 50 km east of Seattle, the South Fork Tolt Reservoir provides approximately one-third of Seattle's water supply. In 1975, the U.S. Environmental Protection Agency (EPA), while studying asbestos contamination in water supplies, discovered that the Tolt Reservoir contained asbestos fibers. Reservoir waters contained both chrysotile (up to 1.6 X 10^6 fibers/liter) and amphibole (up to 1.9 X 10^6 fibers/liter) asbestos fibers with lesser amounts commonly found in tributary streams. However, a point source could not be determined for either type of asbestos, indicating widespread distribution within the watershed (Kirmeyer 1979; Millete et al. 1979).

Many studies have demonstrated a link between airborne asbestos fibers and the increased incidence of asbestosis and various cancers in humans (c.f. Kane 1993). Although gastrointestinal cancer has been linked to occupational asbestos exposure, no definitive data on the effects of drinking asbestos appears to exist for either animals or humans (U.S. EPA 1980; Polissar et al. 1984). Nevertheless, the Seattle Water Department, with a grant from the U.S. EPA, developed methods of filtering asbestos fibers from the water supply (Kirmeyer 1979).

Asbestos appears to be widely distributed within the Tolt watershed and no significant human asbestos-polluting activities have affected the area. This indicates a natural source of asbestos contamination; determining this source could help minimize reservoir water contamination. We conducted a study to determine the natural geologic source of asbestos within the watershed. Asbestiform minerals occur only in specific rock types such as ultramafic rocks that have been metamorphosed and sheared (Deer et al. 1963a and b; Hodgson 1977; Whittaker 1979; Wicks 1979). We considered two possible sources of naturally occurring asbestos: one from bedrock in the watershed and another from glacial materials transported from outside the watershed by glacial and fluvial processes.

Geologic Setting

The South Fork Tolt Reservoir occupies a steep-walled glacial valley which trends east-west and rises from about 500 m in elevation on the valley floor to 1500 m on the adjacent ridges. On the west end of the reservoir, late Pleistocene Puget-lobe glaciation formed a moraine near the present-day dam site. The rest of the watershed shows the effects of Pleistocene alpine glaciation.

Bedrock

There are three major bedrock groups within the South Fork Tolt Reservoir watershed (Figure 1) that have been described by Tabor et al. (1993). Pre-Tertiary melange rocks, composed of metagabbro, metadiabase, metatonalite and argillite, crop out in the center of the watershed. Over-

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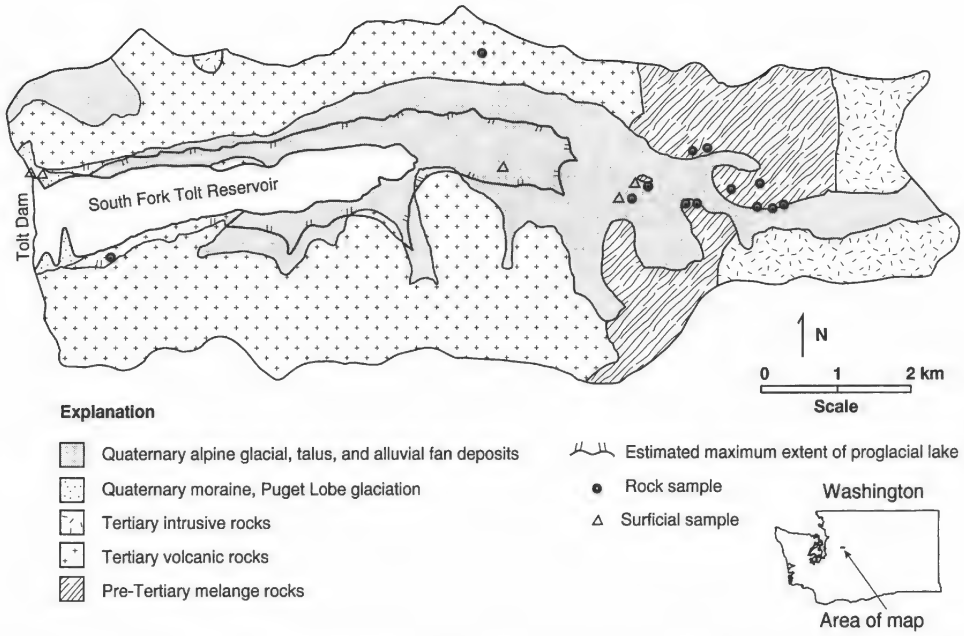

Figure 1. Geologic map of the South Fork Tolt Reservoir watershed showing sample locations. Geologic units adapted from Booth (1990) and Tabor et al. (1993); estimated extent of proglacial lake from Knoll (1967).

lying this group are Tertiary volcanic rocks, predominantly andesites, that are exposed in the western portion of the watershed and surround the reservoir. Intrusive rocks, tonalite and granodiorite from the Tertiary Snoqualmie batholith as well as gabbro, are found in the eastern portion of the watershed. The melange rocks are the only group likely to contain asbestiform minerals. Small ultramafic pods of serpentinized peridotite have been found by Tabor et al. (1993) in melange rocks east of the Tolt watershed (Figure 2). Within the watershed, however, no ultramafic rocks were mapped by Tabor et al. (1993) and none were found during our field investigations.

Glacial history

The history, distribution, and composition of alpine and Puget-lobe drift are described in detail by Knoll (1967) and Booth (1990) and are summarized briefly here. Alpine glaciation in the South Fork of the Tolt reached its maximum extent during the Evans Creek stade of the Fraser Glaciation, before the Vashon Puget-lobe advance. From a probable source in the eastern edge of the watershed, alpine glaciation reached as far west as a bedrock lip near the site of the present-day dam. The broad pass between the eastern edge of the Tolt watershed and the Money Creek drainage was probably occupied by glacial ice, and the ice flow divide may have been east of the present topographic divide.

During the Vashon stade, the Puget lobe of the Cordilleran ice sheet blocked the South Fork Tolt Valley at the rangefront, causing the river to pond eastward behind the glacier. At the ice margin, near the site of the Tolt Dam, glacial drift formed a moraine and meltwater flowed into the proglacial lake. According to Knoll (1967), this lake reached an altitude of at least 600 m, slightly higher than the present-day reservoir level (Figure 1).

Alpine drift

Alpine drift within the South Fork Tolt Valley consists of till, outwash, and glaciolacustrine clays. Alpine till, preserved in tributary stream valleys, extends from the eastern portion of the watershed to near the Tolt Dam. Alpine-derived glaciolacustrine deposits are interbedded with Vashon

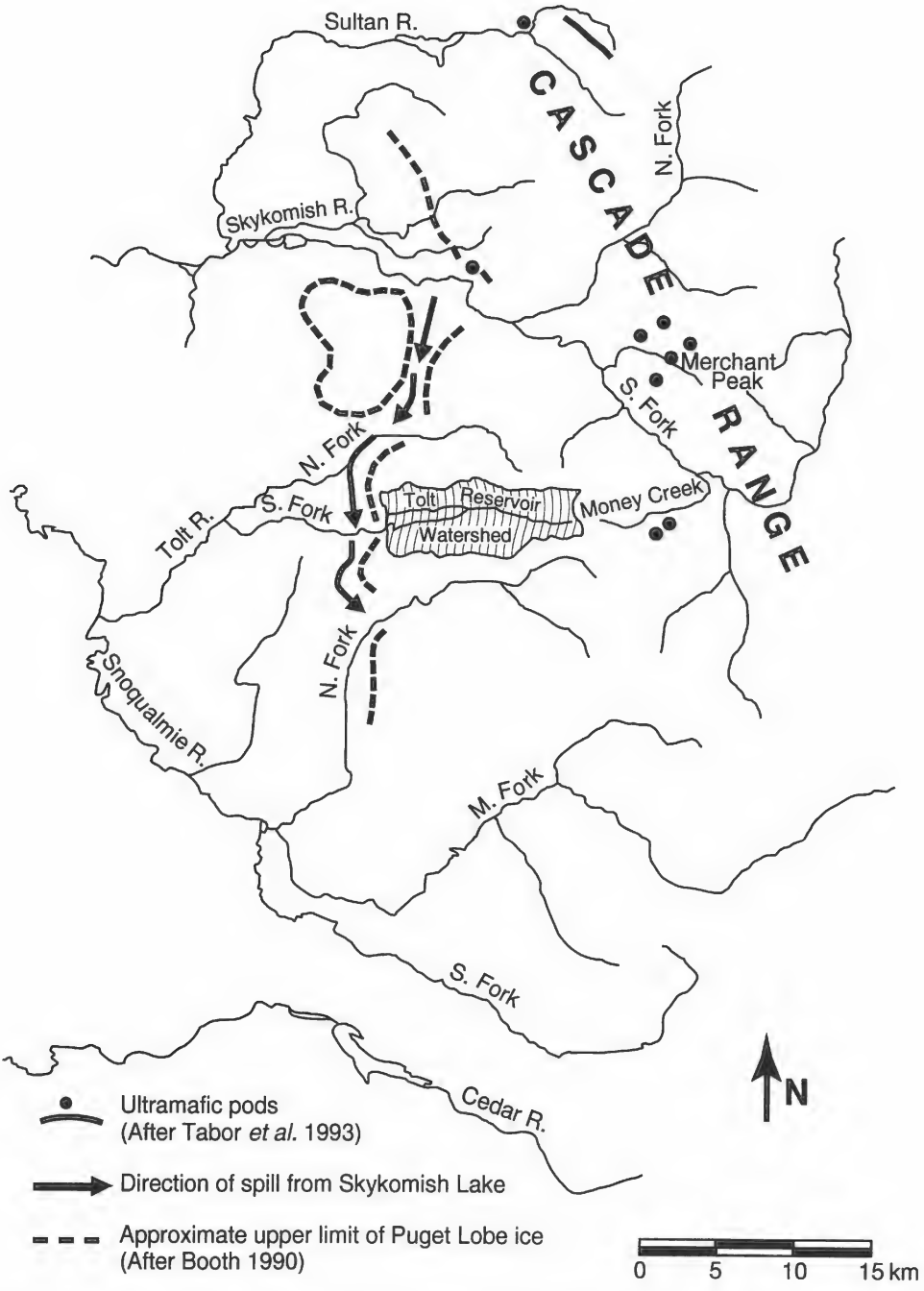

Figure 2. Mapped ultramafic pods, limits of Puget-lobe glaciation, and river drainages near the Tolt Reservoir. Arrows show direction of spill along rangefront from Skykomish Lake during Puget-lobe glaciation (after Booth 1990).

till on the moraine at the rangefront. Blue-gray silty clays overlie alpine till and are divided into two units by Knoll (1967). The lower clays are believed to be composed of proglacial lake sediments derived from alpine material, while the upper clays were deposited by meltwater from both alpine and Puget-lobe glaciers.

Puget-lobe drift

Vashon till from Puget-lobe glaciation occurs in the moraine at the mouth of the valley, along with outwash sands and gravels. The till, composed of rounded gravels set in a clayey sandy matrix, has been traced to an altitude of 700 m at the rangefront. Puget-lobe advance and recessional outwash are exposed southeast of the Tolt Dam. Glaciolacustrine material, partially derived from Puget-lobe glaciation, overlies alpine till near the east end of the reservoir (Knoll, 1967).

Analytical Procedures

We collected and analyzed twenty-three bedrock and exotic cobble samples and six glacial drift samples from the Tolt watershed (Figure 1). Our procedures were designed to verify the presence or absence of asbestos fibers in geologic materials; we did not precisely determine the quantity of fibers present. A complete description of the sampling information and analytical procedures can be found in Reid and Craven (1979).

For selected rock samples, we made and examined thin sections for asbestiform or related minerals. If a sample appeared to potentially contain asbestos, especially chrysotile, we also performed X-ray diffraction and electron microscope scans. We treated glacial deposit samples to remove organics and iron and then particle size separated them using the methods of Jackson (1969). We further separated the silt and clay fractions by density using heavy liquids. Chrysotile, at D ~ 2.55, separated with the light fraction (D < 2.58), while amphibole, at D = 3.0-3.3, separated with the heavy fraction (D > 2.92).

We examined select samples of these density fractions using powder X-ray diffraction (XRD) and scanning electron microscopy (SEM) techniques. Specimens were usually scanned at between 2500 and 5000 X, with greater magnification used to positively identify morphological features and photograph fibers.

Morphological aspects can be very important in determining fiber mineralogy (Asher and Mcgrath 1976; Gravatt et al., 1978). A 3:1 or greater length to diameter ratio is commonly used to define asbestos fibers (U.S. Dept. of Health and Human Services 1980), although asbestiform fibers often have ratios 10:1 or greater. Chrysotile's fibrous form is created by magnesium octahedral and silica tetrahedral sheets rolled into hollow tubes or scrolls (Deer et al., 1963b; Yada 1967; Yada 1971). The edges of the rolled sheets often cause small fibers to have a characteristic groove running along their long axis. Amphiboles tend to form fibers having characteristic cleavage angles (Deer et al. 1963a; Whittaker 1979).

Results

Bedrock

We examined six samples of volcanics, five of metadiabase, four of metatonalite, and eight cobbles of various origins, including gabbros and granodiorites, with the petrographic microscope. We did not observe any asbestiform minerals in the thin sections, although many had stubby, prismatic amphiboles. We also X-rayed the light density fraction of nine samples; none yielded a pattern similar to chrysotile. In addition, we scanned the light density fraction from five specimens (two volcanics, three metadiabases) using the electron microscope and no fiber morphology was observed. We found no asbestos in the twenty-three rock samples examined.

Glacial drift

We performed XRD analysis on three clay and three silt-sized, light-density fractions from Vashon till, glaciolacustrine clay, and alpine till. The diffraction patterns obtained from these yielded indeterminate results. While the patterns closely resembled chrysotile, other minerals (most notably kaolinite) have similar patterns. SEM analysis later revealed the greatest proportion of these samples to be kaolinite-like plates. Under these circumstances, XRD could not confirm or deny the presence of chrysotile. Similar problems have been encountered by other workers (Mangia 1980). XRD detection limits for chyrostile or amphibole asbestos in mixtures with other minerals are in the 0.5 to 2 wt. % range (Guthrie 1993).

We scanned the light and heavy density fractions from both silt and clay sizes of six glacial drift samples using SEM methods. Specimens prepared from the Vashon moraine, outwash, and glaciolacustrine material showed the highest amounts of both chrysotile and amphibole fibers. Lesser amounts of chrysotile and amphibole asbestos fibers were found in alpine till from a location below 640 m in elevation. No asbestiform minerals were found in the upper alpine moraine material. All heavy density fractions also contained some non-asbestiform amphiboles.

Discussion

Distribution of asbestos within the watershed

In bedrock within the South Fork Tolt Reservoir watershed, we found no evidence of asbestos. However, all materials derived directly from the Puget-lobe glaciation that we examined contained both chrysotile and amphibole asbestos. Two "mixed" samples (alpine till below the Vashon-age lake level) also contained chrysotile and amphibole fibers, though in conspicuously lesser amounts than Vashon till, outwash, and glaciolacustrine sediments. In addition, chrysotile and amphibole asbestos streamwater concentrations reported by Kirmeyer (1979) indicate that tributaries in contact with Puget-lobe drift or glaciolacustrine sediments contain asbestos fibers. Of these tributaries, higher asbestos concentrations were found in those in the western portion of the watershed.

Within the watershed, asbestos fibers are distributed in glaciolacustrine sediments. This makes the extent of the Vashon-age proglacial lake a significant factor influencing the extent of asbestos distribution. Knoll (1967) found evidence that the lake reached an altitude greater than 600 m (Figure 1). Vashon till has been traced to an altitude of 700 m near the dam of the proglacial lake. In principle, the maximum possible lake level could be close to that altitude, although there is apparently no direct sedimentary or geomorphic evidence to support this. We found asbestos fibers in a sample of "mixed" alpine till taken from a streamcut at approximately 640 m elevation, suggesting that either previous continental glaciation or the proglacial lake level reached this elevation.

In the Tolt watershed there is little chance of physically isolating asbestos-bearing materials from the water supply because glaciolacustrine materials, partially derived from Puget-lobe glaciation, were used to seal the reservoir. Any activity that increases erosion and mass wasting of these widespread, unconsolidated materials within the watershed would likely increase waterborne asbestos.

Source area of asbestos

The bedrock source of the asbestos found in the Puget-lobe drift probably lies to the north of the Tolt watershed, in the North Cascades. The North Cascades contain widespread serpentinized ultramafic pods, some of which have asbestiform minerals (Misch 1966; Vhay 1966; Brown 1987; Tabor et al. 1993). North of the Tolt reservoir, the Pilchuck, Sultan, Stillaguamish, and Skagit Rivers all drain terranes of the North Cascades, and all contain asbestos from indigenous sources (D. Dethier, oral communication 1979). During the Vashon-age glaciation, asbestiform minerals probably reached the Puget lobe from sources in the Cascades by combined alpine glacial and fluvial processes. However, significant southward glacial transport of this material was probably minor. Most Puget-lobe drift only contains 5-15% clasts foreign to the local drainage (Booth 1990).

Within the South Fork Tolt watershed, no ultramafic rocks are known to crop out, although some may occur under surficial deposits. Tabor et al. (1993) mapped ultramafic rock occurrences about 5 km east of the watershed above Money Creek and about 10 km northeast of the watershed in the Merchant Peak area of the Skykomish River watershed (Figure 2). Alpine glacial transport of ultramafic materials from the Money Creek watershed over the broad pass into the eastern Tolt watershed is unlikely because the required ice flow divide would have been located in an area of the Money Creek drainage that is presently about 5 km east of and 400 m lower than the pass.

The most likely source of asbestos is the Skykomish watershed, with transport to the Tolt watershed by Puget-lobe glacial or glaciofluvial processes (Figure 2). During the complex recessional history of Vashon-age glaciation, water draining from north and east of the Skykomish valley was impounded in a lake occupying the

Skykomish valley (Booth 1990). This lake would have collected water and sediment from areas with known ultramafic pods such as the Merchant Peak area and the Sultan River basin to the north. During most of the Vashon-age glaciation, the only drainage from this lake spilled southward through a trough along the rangefront, eventually reaching the Snoqualmie watershed south of the Tolt (Figure 2). Subglacial and subaerial passageways in this trough provided some of the sediment found in recessional deposits downstream from the present day Tolt reservoir (Booth 1990). Flow from the Skykomish valley lake probably provided sediment, and with it asbestos, to the proglacial lake then occupying the South Fork Tolt reservoir site.

Regional significance

Asbestos-bearing ultramafic rocks in watersheds of the North Cascades may provide a naturally-occurring source of asbestiform minerals. In the South Fork Tolt Reservoir watershed, our results strongly indicate that both chrysotile and amphibole asbestos fibers were transported into the watershed by Puget-lobe glacial and glaciofluvial processes, and were not derived from any bedrock source within the watershed. The occurrence of asbestiform minerals in widespread Puget-lobe glacial materials has regional significance beyond the Tolt Reservoir watershed. For example, the north forks of the Tolt and Snoqualmie Rivers also were found to contain asbestos at the same time that asbestos was discovered in the Tolt Reservoir (Seattle Water Department, unpubl. data). In these watersheds, asbestos may also have been transported southward from the Skykomish drainage. Further south, the Cedar River, Seattle's other water source, contains only minor amounts of asbestos (J. Sceva, oral communication 1979). This watershed is not underlain by melange or ultramafic rocks (see mapping by Frizzell et al. 1984); moreover, it was not directly affected by drainage from the Skykomish valley. Thus, both the distribution of asbestos-bearing rocks and the distribution of Puget-lobe glacial materials influence the likelihood of natural asbestos minerals occurring in the waters or sediments of other watersheds in the Puget Sound area.

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Seasonal and Long-Term Variations in Water Quality of the Columbia River at Revelstoke, B.C.

Abstract

The purpose of this study was to analyze six years of water quality data collected every four weeks from the Columbia River at Revelstoke to determine the processes controlling water quality and the presence or absence of trends. Plots versus time were used to assess seasonality, while hysteresis diagrams were used to describe processes affecting the water quality variables through the relationship of water chemistry to discharge. The major ions exhibited seasonality showing high concentrations in the winter and low concentrations in the summer, while other variables did not exhibit seasonality. The hysteresis diagrams indicate that the seasonal pattern of major ions is different from natural systems. The lack of flow relationships for metals and other sediment related variables also differs from natural systems. These differences result from impact of reservoirs on the river processes. Box-Jenkins time-series techniques were used to model and forecast future values for the variables. Revelstoke Dam has a significant impact on the water quality processes. No trends over time were found for the water quality variables.

Introduction

When attempting to assess if any trends are present in the water quality of a watershed, it is important to consider the impact of the surrounding environment, both natural and man-made.This is necessary to answer the two dominant questions in the study of water quality: (1) Why is the quality of the river as observed? and (2) Is the water quality changing over time? The presence of Revelstoke and Mica Dams significantly alters the flow regieme of the Columbia River. These impacts must be considered in any study of water quality variables downstream from these developments. Whitfield and Woods (1984) studied the impact of the construction of the Libby Dam on the Kootenai River below the dam and found that the dam regulated flow and reduced the seasonality of hydrologic and water quality variables.

Hysteresis diagrams are useful in evaluating how water quality variables behave in relation to discharge (Whitfield and Whitley, 1986; Whitfield and Clark, 1992). Plotting the concentration of a water quality variable versus discharge reveals patterns which can be compared to known classifications. Williams (1989) provides one classification which has five typical relationships which can be used to identify hydrological characteristics of a variable. In natural systems, these diagrams have been shown to be useful in determining processes which control water quality (Whitfield and Whitley, 1986; Whitfield and Clark, 1992; Bhangu and Whitfield, in press).

To determine whether a short or long term trend is present, time-series analysis is utilized. Time series analysis permits the statistical evaluation of data which are not independent and uncorrelated over time. For a time-series of dependent data, model results can be used to forecast future values, which can then be studied for evidence of a change in the mean of a series (Chatfield, 1984). Bhangu and Whitfield (in press) used both hysteresis diagrams and time-series analysis to study trends at the Skeena River at Usk; much the same process has been followed here.

This study uses six years of water quality data gathered from Columbia River at Revelstoke (Environment Canada Station Number -BC08ND0002), downstream from the Revelstoke Dam. The data, collected every 28 days from January 1986 to December 1991, were used to construct Box-Jenkins time-series models. Data from January 1992 to April 1993 were used independently to check the accuracy of the model and validate the results.

Study Area

The features of the upper Columbia watershed are identified in Figure 1. The Columbia River arises in Columbia Lake in southeastern British Columbia and flows northwest before bending

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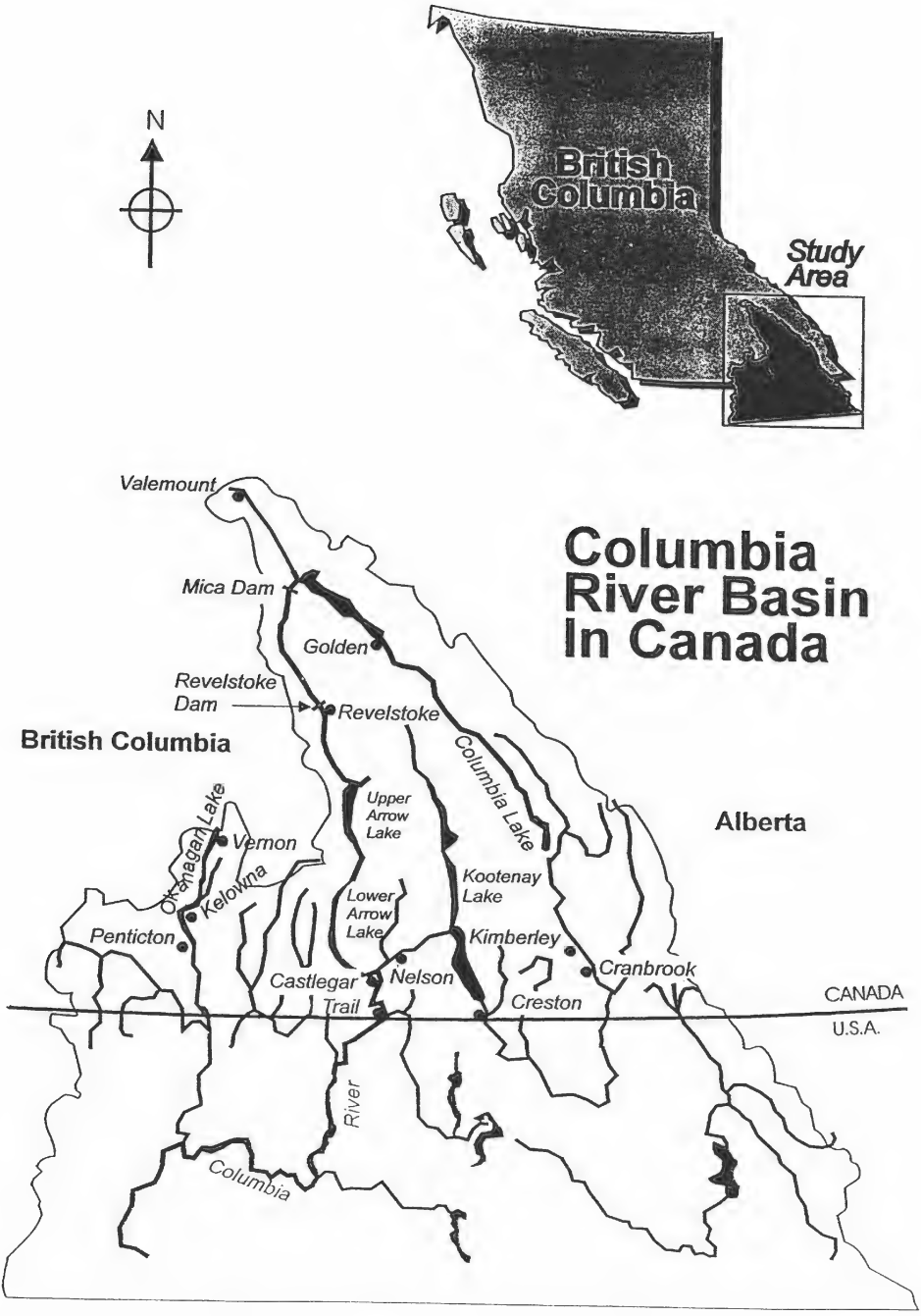

Figure 1. Columbia River basin in Canada showing the drainage area considered in this study.

south again to continue through the United States where it drains into the Pacific Ocean at Astoria, Oregon (Columbia River Treaty Permanent Engineering Board, 1992). The area of interest is the portion of the river upstream from Revelstoke, B.C., which has a drainage area of approximately 26,700 km^2.

The Revelstoke Dam is located 5 km north of the city of Revelstoke. The dam began operation in 1984 and creates a reservoir which extends north to the Mica Dam (B.C. Hydro, 1993). This reservoir, called Lake Revelstoke, provides increased energy capability. Located about 130 km north of Revelstoke Dam is Mica Dam. Drainage area above the Mica is 21,000 km^2, comprising the majority of the flow of the study area. The Dam became operational in 1973 as part of the Columbia River Treaty. This treaty, signed and ratified in 1964, is an agreement between the governments of the United States and Canada to jointly supervise and maintain the development of the Columbia River basin. This included the construction of the Mica, Duncan and Keenleyside Dams in B.C. and the Libby Dam in Idaho (Environment Canada, 1975).

Methods

i. Data Sources

The water quality monitoring station is located on the Trans-Canada Highway bridge 5 km downstream from Revelstoke Dam. This site is operated under the Canada-British Columbia Water quality Monitoring Agreement. The collection of data under this program is described by Clark and Whitfield (1993). The water quality variables were analyzed using standard methods (Environment Canada, 1979).

Six years of data were used in this analysis. Variables were eliminated from the study if there were large amounts of missing data or if there was little or no variation. Of the 55 initial variables listed, 21 had enough data and spread for examination. These were: discharge, lab pH, specific conductivity, turbidity, total alkalinity, calcium, magnesium, hardness, potassium, sodium, chloride, silicate, sulphate, copper, iron, lead, manganese, and zinc. The dissolved form of the major ions were measured, as were the total form of the trace metals. Nitrate+nitrite, total phosphorus, and total dissolved nitrogen each had three repetitions. Each of the three replicates were treated as a completely separate variable, bringing the total to 27 time series analyzed.

For each variable, a time-series plot was prepared with the water quality variable on the y-axis and time plotted on the x-axis. This gave a good representation of how water quality behaved during the time period and displayed any unusual data, or outliers, which could damage the accuracy of a forecast. These plots also displayed the degree of seasonality existing in each variable, which assists in fitting a time-series model to the data.

ii. Process Analysis

Hysteresis plots were then created to evaluate if there is a relationship with discharge. These log-log plots of water quality versus discharge for a typical year are useful in determining processes affecting water quality and the timing of peaks. A positive slope indicates a positive relationship with discharge, a negative slope indicates an inverse relationship to discharge, and no slope indicates no relationship to discharge.

iii. Trend Assessment

To utilize Box-Jenkins time-series models, the data must be stationary. In fitting a Box-Jenkins model all significant trends and seasonality are removed and in the resulting series there must be stationarity [i.e., no systematic change in the mean] (Chatfield 1984). The plots of water quality versus time are used with the autocorrelation and partial autocorrelation function of a series to determine if there is a trend present. Trends and patterns found in the series can be rendered stationary by applying a linear difference operator. For all the series considered, a seasonal model was adequate (as there was 13 observations per year the differencing was lag 13).

Afterwards, the autocorrelation and partial autocorrelation functions of the differenced series are checked to assure that all seasonality has now been removed, and are then used to identify a tentative model for the data. These models typically contain moving average (MA) and autoregressive (AR) terms. Future values are then forecasted based on the model. These values are plotted versus the observed results to visually confirm that the model is adequate. Residuals are then checked to ensure results are reasonable.

Results and Discussion

i. Process Analysis

Minimum and maximum values for each of the water quality variables observed during the study period and the Canadian Standards for Drinking Water and Aquatic Life are provided in Table 1. The variable with the largest range was iron which had a maximum value of 8.33 mg/L and a minimum value of 0.036 mg/L - a 231 fold range. Most of the other variables also show significant variation with the maximum values being from two to ten times greater than the minimum. Of the variables where a standard exists, all the variables except iron and lead were less than both the Drinking Water and Aquatic Life Standard (Table 1). Iron and lead exceeded the standard only during periods of high discharge associated with high levels of sediment.

Some of the observed variables, such as apparent colour, did not have enough variation to be used in trend assessment, while others showed considerable spread. This showed up more clearly in the time series plots. Strong seasonality was observed in only six of the variables: alkalinity, calcium, hardness, specific conductance, magnesium, and sulphate.

These variables were similar. Peaks were observed with the high concentrations typically occurring in the February-April range and lows in July or August. The exception was sulphate which had inconsistent high concentrations between years, but consistently had an annual low in July or August of each year. The rest of the variables showed little seasonality and no other trends. The fact that these six variables are major anions and cations seems to indicate that seasonality might occur more often in this group than other water quality variables in rivers controlled by reservoirs.

Another characteristic of these variables was the presence of one year of data which stood out from the rest. Between July 1989 and July 1990, each of the plots displayed a period with shortened peaks and less variation. This period did not seem typical and was not used for hysteresis plots and was omitted from the forecasting process when possible. Figures 2-4 demonstrate the nature of the seasonal patterns these variable demonstrate over the study period.

Hysteresis plots were prepared for each variable and each of the six years of the study. In addition, plots of the variables with discharge versus time were used to demonstrate any relationship to discharge. Figures 5 and 6 show these plots for calcium and alkalinity. The group of major ions mentioned above all exhibited a negative relation with discharge. This same result was found by Bhangu and Whitfield (in press) in the Skeena River at Usk and by Whitfield and Whitley (1986) in the Yukon River Basin. However, the pattern we observed was quite distinctive. The hysteresis diagrams show a linear portion at low flow with an open loop at high discharges.

Hysteresis plots for the other water quality variables did not reveal any measurable relationship

TABLE 1. Ranges of water quality variables observed in the Columbia River at Revelstoke during the study period.

Variable	Minimum	Maximum	Standard*
PHYSICAL			
Discharge (m^3/s)	245	1600	
Turbidity (FTU)	0.1	4	
Specific Conductance (µS/cm)	95	151	
pH	6.7	8.2	6.5-8.5/6.5-9.0
Apparent Colour (relative units)	5.0	15.0	
Air Temperature (°C) (at time of sampling)	0.0	20.0	
Water Temperature (°C)	0.0	12.0	
MAJOR IONS (mg/L)			
Total Alkalinity	38.0	64.1	
Calcium	12.9	21.1	
Potassium	0.4	0.7	
Sodium	0.5	1.4	200/
Chloride	0.2	0.6	250/
Hardness	43.1	75.1	
Sulphate	7.1	13.9	500/
Magnesium	2.6	5.5	
NUTRIENTS (mg/L)			
Nitrate+Nitrite	0.003	0.73	45.0/
Total Dissolved Nitrogen	0.118	0.85	
Total Phosphorus	0.002	0.4	
TRACE METALS (mg/L)			
Total Iron	0.036	8.33	0.3/0.3
Total Lead	0.0002	0.0078	0.01/0.007
Total Zinc	0.004	0.11	5.0/0.03

* Canadian Drinking Water Standard/Freshwater Aquatic Life

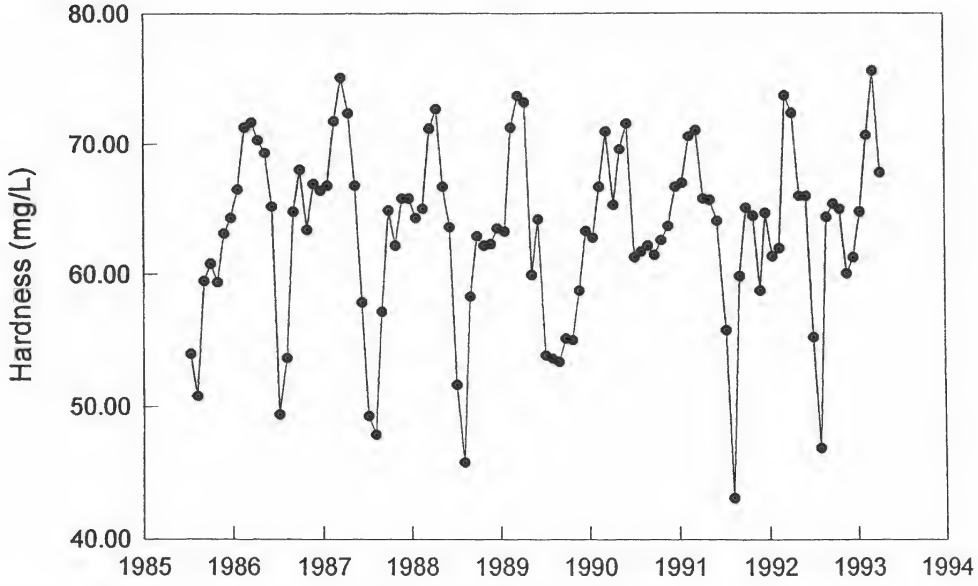

Figure 2. Time series plot of hardness (mg/L) from the Columbia River at Revelstoke.

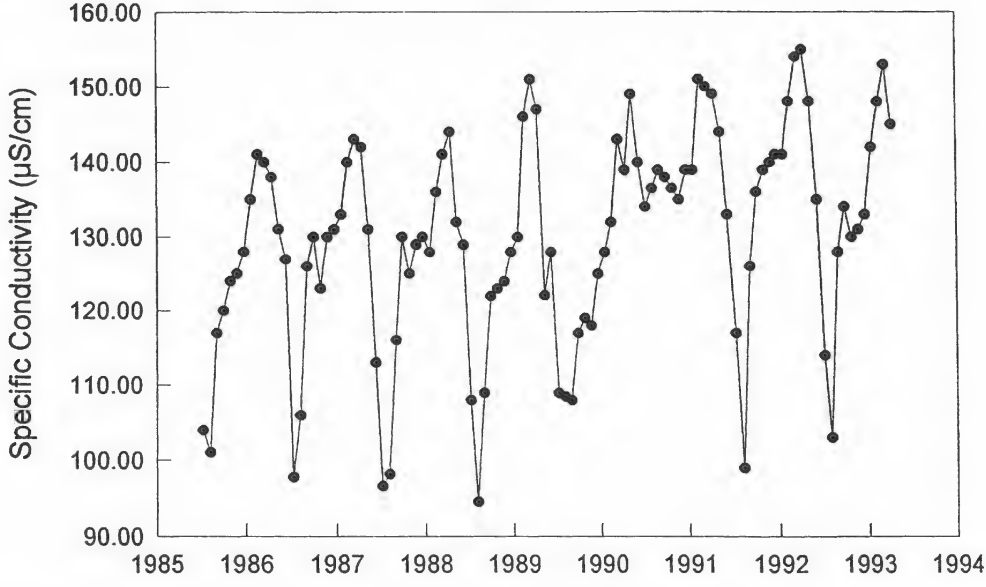

Figure 3. Time series plot of specific conductance (µS/cm) from the Columbia River at Revelstoke.

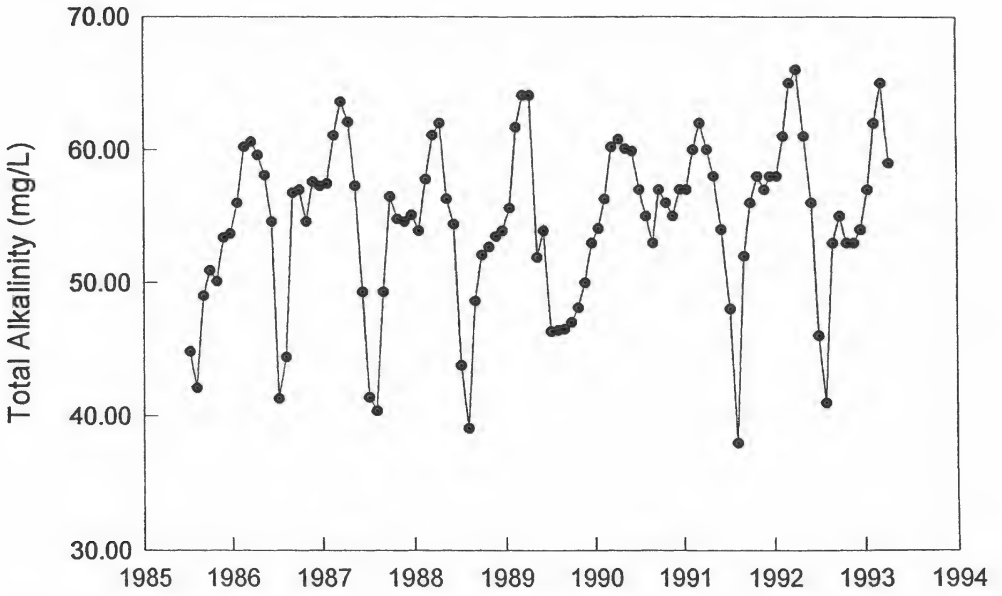

Figure 4. Time series plot of total alkalinity (mg/L) from the Columbia River at Revelstoke.

to discharge. Figures 7 and 8 show the negative relation between concentration and discharge for total alkalinity and calcium. These results are typical of all the major ions we examined. The hysteresis for these 6 major ions had a slightly negative slope, on a logarithmic scale, with a counter-clockwise loop at the end. The slope was less steep than expected. The postulated mechanism behind this, suggested by Whitfield and Whitley (1986), is as follows: snowmelt and surface runoff dilute groundwater during freshets; during post-freshet conditions concentrations increase with the increasing dominance of groundwater. The shape falls into Williams (1989) "single line plus a loop category", and signifies that during the period of the year where discharge is low and concentration is high the curves are in phase. However, during the high discharge period a loop occurs because concentration reaches a low before discharge reaches the peak. This can be witnessed by the first year in Figures 5 and 6; both calcium and alkalinity hit a low peak just before discharge hits a high peak, creating the loop observed in the hysteresis plots. Hysteresis plots for alkalinity and calcium are shown in Figures 7 and 8. In natural streams, these variables typically exhibit an open clockwise loop with no linear feature (eg. Whitfield and Whitley, 1986; Whitfield and Clark, 1992; Bhangu and Whitfield, in press). In 'natural' systems throughout British Columbia and the Yukon the hysteresis plots for anions and cations are open loops (Whitfield and Whitley, 1986; Whitfield and Clark, 1992; Bhangu and Whitfield, in press). In the Columbia River at Revelstoke these plots show linear portions (Figures 7 and 8) which are the result of the mixing of water which take place within the reservoir and causes the discharge and concentration curves to be in phase during the winter.

Silicate and pH were independent of discharge, appearing as a line which was horizontal across a range of discharges. Both these variables had a counter-clockwise loop at the high discharge end. Nitrate+nitrite, total phosphorus, total nitrogen, chloride, copper, iron, lead, zinc and manganese all had no clear shape and were independent of discharge (i.e., no slope).

In the study of discharge and water quality in the Yukon River basin, Whitfield and Whitley (1986) observed that the variables of lake-fed systems had "low-slope" relationships to discharge more noticeably than river-fed systems. As this system is fed by the Revelstoke reservoir, it is "lake-fed" and exhibits similar behaviour. The

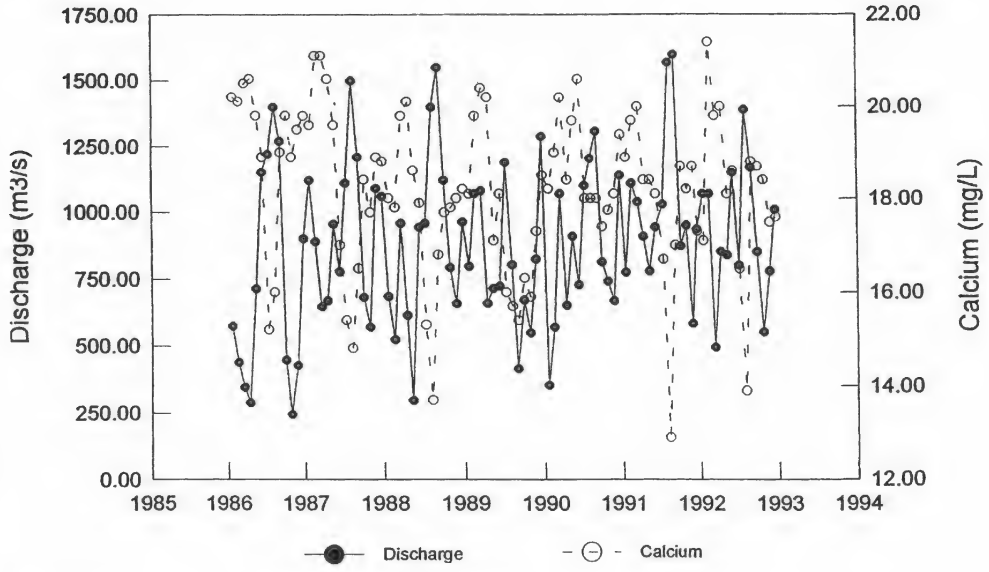

Figure 5. Time series plot of discharge (m^3/s) and calcium (mg/L) from the Columbia River at Revelstoke.

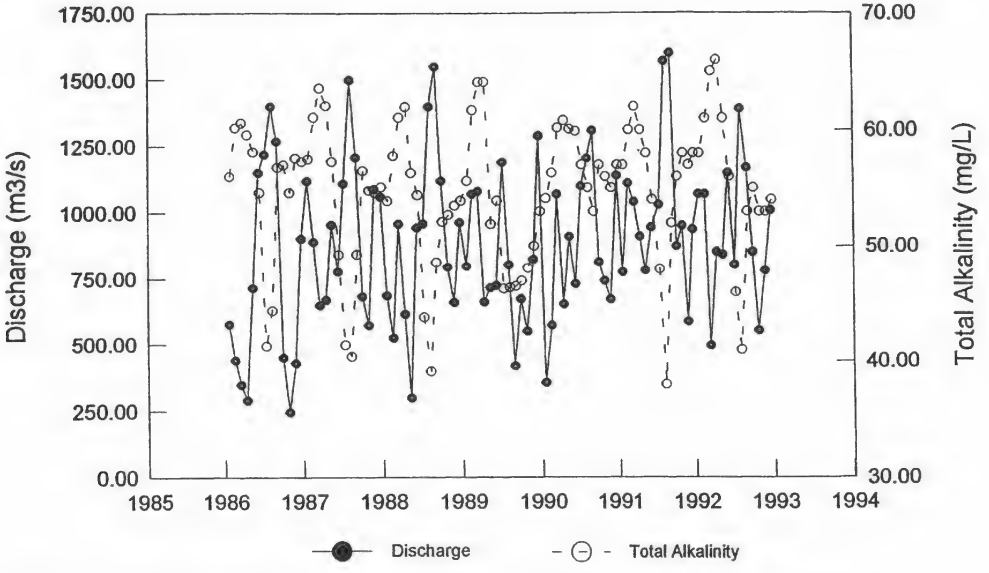

Figure 6. Time series plot of discharge (m^3/s) and total alkalinity (mg/L) from the Columbia River at Revelstoke.

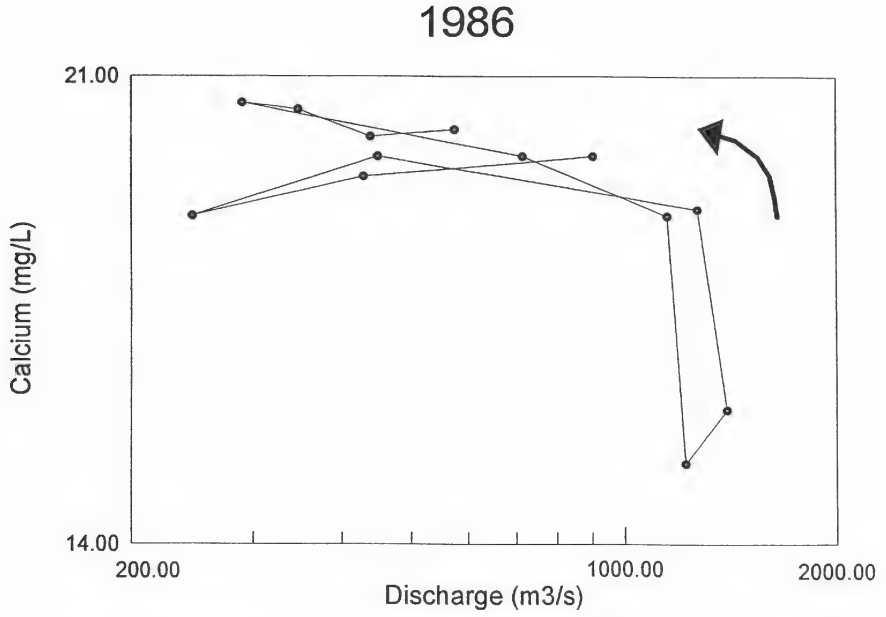

Figure 7. Hysteresis plot of calcium from the Columbia River at Revelstoke.

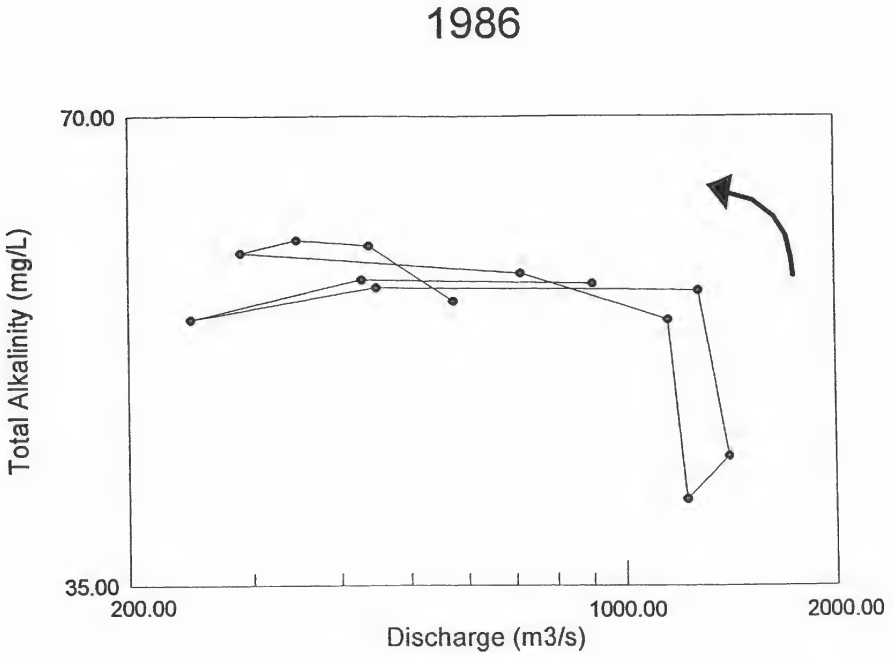

Figure 8. Hysteresis plot of alkalinity from the Columbia River at Revelstoke.

suggested reasons for this are the buffering and trapping processes in lakes, which result in the simple dilution of a uniform concentration (i.e., the lake water) as the prominent mechanism.

ii. Trend Assessment

As the first step in trend assessment we examined time series plots of water quality variables to see if there was any obvious trend which might continue into the future. None of the variables analyzed displayed an obvious trend, and the series appeared to have a stationary mean. The time series plots also showed that the data between July 1989 and July 1990 was different from other years. During this period, discharges in the Columbia were reduced through storage of runoff behind Mica Dam, altering the normal year to year flow patterns (eg. Figure 5). The result of this, for the water quality variables, is that the low concentrations normally observed during the peaks of discharge are absent from the record in this period.

Following the time series plots, Box-Jenkins time-series methods were used on the stationary series to find a model which fit the existing series and then could be used to forecast future values of a time-series and thus future trends. There were various problems which stopped models being fitted to certain variables. Total aluminum, mercury, selenium, barium, arsenic, nitrate+nitrite, total dissolved nitrogen, total phosphorus, turbidity, sodium, chloride, and fluoride all had so little variation that reliable time-series models could not be fitted. These variables could be simply expected to continue as observed. Silicate and total copper had missing data which disrupted the modelling process. The series of pH contained a period where the data obtained was known to be questionable, so a model was not fitted.

Models were fitted for the same six major ions studied previously as well as discharge. The resulting models are listed in Table 2. None of the models needed a trend component, indicating that we are currently observing no trend in the water quality. These models contain both an autoregressive component and a seasonal moving average component, indicating that over time samples which are close together in time are similar (autoregressive component) and samples which are one year apart are similar (seasonal moving average).

Alkalinity, hardness, specific conductance, magnesium, calcium and discharge were all differenced for stationarity, and then fitted with a multiplicative autoregressive model with lags at 1 and 13, indicating that each value is dependant on the previous value and the value 13 observations (one year) ago. This is the seasonal effect. The forecasts from the fitted models for alkalinity, magnesium and hardness are in Figures 9, 10, and 11. For sulphate, an autoregressive integrated moving average, or ARIMA, model with an AR term at lag 1 and an MA term at lag 13 was identified.

TABLE 2. Summary of Box-Jenkins Models fitted to water quality variables from the Columbia River at Revelstoke.

Water Quality Variable	Model[1]
Sulphate	ARIMA $(1,0,0)(0,1,1)_{13}$
Alkalinity	ARIMA $(1,0,0)(1,1,0)_{13}$
Hardness	ARIMA $(1,0,0)(1,1,0)_{13}$
Specific Conductivity	ARIMA $(1,0,0)(1,1,0)_{13}$
Magnesium	ARIMA $(1,0,0)(1,1,0)_{13}$
Calcium	ARIMA $(1,0,0)(1,1,0)_{13}$
Discharge	ARIMA $(1,0,0)(1,1,0)_{13}$

[1]Model notation as described by Box and Jenkins (1976).

The plots of the forecasted versus observed values illustrate the expected inadequate fit in the 1989-90 year. After this period, however, the forecasts fit the observed values, indicating that this period of time was indeed abnormal. All forecast series showed no trends or other changes in the immediate future.

Conclusions

The Columbia River at Revelstoke exhibits distinct patterns of water quality. These patterns are the result of the modification of the natural system by the reservoirs upstream of the study site. These effects were prevalent durng the winter low flow period when the natural pattern of concentration and discharge being out of phase was changed to a pattern of being in phase. Major ions exhibited distinct seasonality and these ions varied inversely with discharge. The seasonality normally observed for variables typically associated with sediment has been dampened out in the reservoir behind the dam. The ARIMA models fitted to the series of water quality did not include a trend component indicating that no trends in water quality are occurring in the Columbia

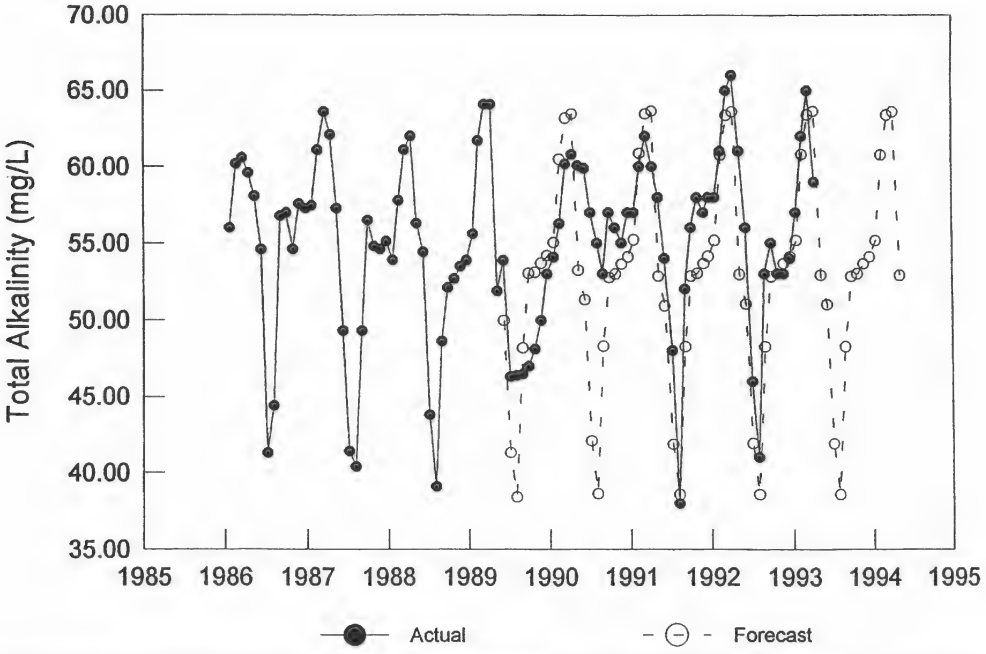

Figure 9. Actual and forecast alkalinity concentrations based on the fitted Box-Jenkins model for the Columbia River at Revelstoke.

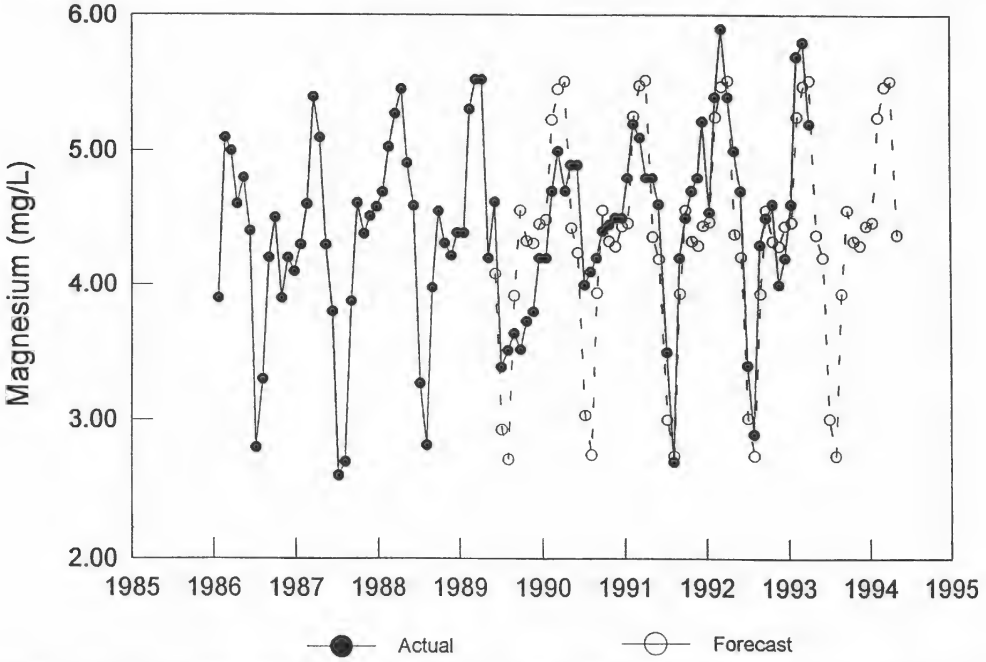

Figure 10. Actual and forecast magnesium concentrations from 1986 to 1994 based on the fitted Box-Jenkins model for the Columbia River at Revelstoke.

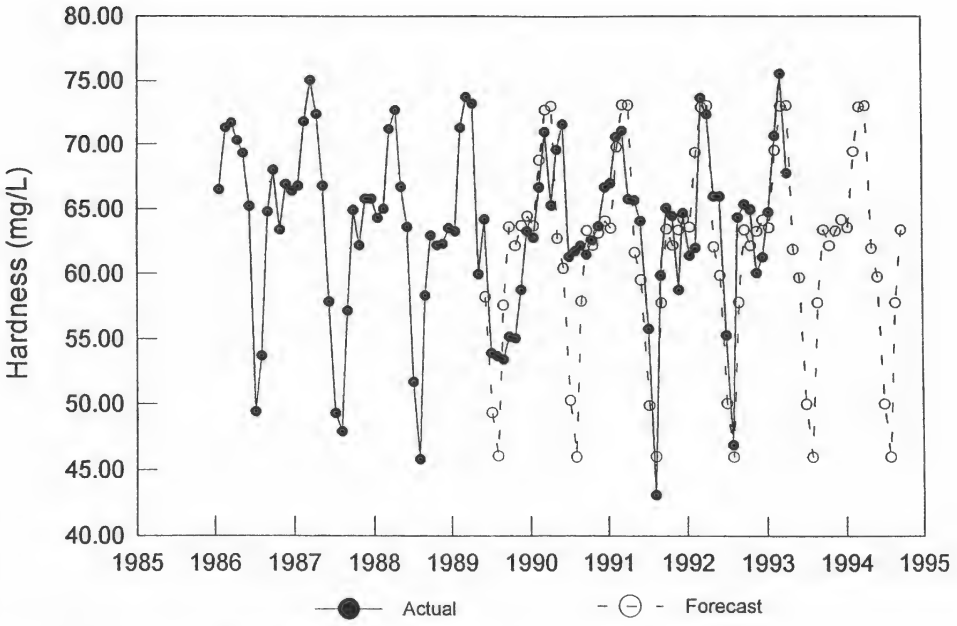

Figure 11. Actual and forecast hardness concentrations based on fitted Box-Jenkins model for the Columbia River at Revelstoke.

River at Revelstoke at present. Processes currently occurring are forecast to continue into the near future.

Acknowledgements

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Northwest Science Forum

Northwest Science Forum provides an opportunity to articulate and discuss scientific issues in a less structured format than peer-reviewed articles. The Forum publishes short articles, opinion pieces, and letters with a focus on science and natural resource issues in the Pacific Northwest. Although the Forum is not peer-reviewed, it is edited for format and clarity. Articles should generally be less than 2000 words and contain minimal literature citations. Letters in response to articles are particularly encouraged; the original author will normally be given a chance to respond to the letter as well. There are no page charges or reprints associated with the Forum, and participants need not be members of the Northwest Scientific Association. Please send all submissions, including two hard copies and an electronic copy (any recent version of Word or WordPerfect, Macintosh or DOS), to the Editor.

Margaret A. Shannon and **Alexios R. Antypas,** College of Forest Resources, University of Washington, Seattle, Washington 98195-2100

Civic Science is Democracy in Action

January 1945, Lonepine Montana

Upon the invitation of Mr. Halvorsen we have come here to help you organize a Lonepine study group, in which you may analyze and look into the problems of your community. We are not thinking in terms of an action committee, but a group that will uncover whatever problems exist, study their underlying causes and effects, and engage in objective, friendly discussion with a view toward solving them. (Poston 1950:40).

With World War II raging across both oceans, people living in small isolated communities in Montana came together in the evenings, sometimes with university scientists, to do research on themselves, their communities, their state and their world. Their purpose was simple: the forces creating the modern industrial nation and economy were draining rural communities of people, money and resources. To survive and maintain their community, action was needed. But what kind of action and by whom?

The core principle of democracy is that educated citizens should make decisions about how to govern themselves. Segregating science and education into specialized settings like universities where professional researchers study and teach undermines the democratic capacity of citizens. From the perspective of rural communities during all of the 20th century, universities have trained young people for careers in cities, agencies, or other distant places. Indeed, it is generally argued that with declining rural economies such training is necessary to provide opportunities for employment. But from the perspective of a healthy, active democracy, the separation of science and education from daily community life threatens the foundations of a self-governing society.

This paper takes up the issue of science and scientists as contributors to creating **civic science** for a learning and experimenting society. Democracy is designed as an experimenting process in that it works by trial and error. Solutions to problems are developed in response to creative ideas and then tested. What works is kept, what doesn't is redesigned based upon experience. These ideas are deceptively simple! We all know that many "solutions" become so entrenched as to be permanent fixtures, often with permanent ways of getting around them. Problems are often ideologically defined, and thus allow only a narrow range of potential solutions to be considered. Changing laws, rules and policies or funding commitments takes serious effort, often over long periods of time or in the face of definitive failure.

So how do we improve democratic capacity in the face of such obstacles? The first and easiest step is by taking science out of the universi-

ties and research institutions and putting it back in the hands of citizens. By this we do not mean simply moving laboratories to the hinterlands, but rather reconceptualizing *what science is, who does it, and with what effect*. The notion of scientists as professionals whose specialized training gives them the authority to create scientific knowledge which is separate and distinct from the knowledge of experience and practice rose in prominence in the early 20th century. Around the country universities and colleges were created to develop the knowledge needed for an increasingly technical, industrial society. Even in farming and forestry, the knowledge of practice and experience was discredited and the "scientific" knowledge of experts given prominence and new social authority. When "modern industrial methods" of farming or forestry led to social, eocnomic, or ecological problems, new technical experts were called to fix them. The voices of experience and history were silenced and ignored.

What Is Civic Science? Why Is It Different?

Contemporary science and contemporary democracy are both distinctively modern institutions. By modern we mean, progress in society through improvements in science and technology leads to better lives for all. Thus, while firmly grounded in ancient antecedents, science and democracy are institutions of modern society with shared values and assumptions about the importance of progress. Of course, a commitment to progress brings an acceptance of continual change as a way of life. This is in contrast to traditional societies in which knowledge, especially through religion, had the central purpose of keeping the pattern of social life constant.

The challenge of defining civic science lies in distinguishing it from the scientific institutions created in the 19th and 20th centuries. In other words, the most important barrier to a fully developed civic science is how science is currently carried out and by whom! It is neither method nor subject that is the problem here. Rather it is the implicit agreement between the scientific and political communities which gave scientists autonomy and financial support to make discoveries, create knowledge and provide technology to the world. In return the political community freed scientists of responsibility for the consequences of their work, instead taking responsibility upon itself or giving it to "society" in general. This has led to a situation in which scientists are not held accountable for the moral implications of what they do and society can abide by the myth that the social effects of science and technology are pre-determined results, not choices. That is, the effects science and technology are thought to be inevitable, and thus not subject to rational social control but merely requiring social adjustment to them. This double evasion of responsibility thus masks the dynamics of power that permeate the scientific enterprise and also diminishes the ability of a scientifically and technologically advanced society to direct itself and control its destiny. In the end, when scientists find themselves misunderstood or perhaps resented and society finds itself faced with unforeseen ecological and other problems, neither scientists nor citizens are well-served.

Civic science seeks to reunite these divided roles and responsibilities. In civic science we do not just possess knowledge of a detached and objectified world, but are involved in the creation of a better, more meaningful and more fulfilling one. In other words, the world is subjectified as the scientist-citizen and citizen-scientist participate together in its creation. Whereas academic science is oriented toward observation and control, civic science involves observation but is oriented toward interpretation (of nature and society) and involvement. It thus becomes a part of the world rather than a process of standing away and looking at it from a distance.

To democratize science is to bring science back into its proper context. That is, to insure its relevance and morality through involvement with social action. Simultaneously, civic science revitalizes democracy by making citizens more aware and understanding of each other and their world. The proper context of science is as a catalyst for social learning—or, learning about the world that leads naturally to action. Thus, civic science helps make science more meaningful and ethical as well as deomcracy more purposeful and effective.

Who Does Civic Science?

On the evening of April 23, 1945... the Darby Study Group was organized... In addition to the weekly question committees and temporary research committees called for in the study guide which Lonepine helped improve, it was now suggested that two or three standing committees be appointed to investigate the communityís major long range problems. Thus, the group established committees on small industries, local

taxation, and Darby education and recreation. ...For thirteen consecutive weeks nearly thirty resolute citizens gathered around a table in their community hall and sized up the problems of their town." (Poston 1950:52-53).

Can only those located in universities or research groups be called scientists? If so, democracy is in danger. Civic science is essential for active democracy in our communities. The concept of civic science assumes that one essential role of citizens is as lay scientists who seek to clearly, objectively, and honestly assess themselves, their communities, and their society. Moreover, an essential role of scientists is to be engaged as citizens bringing their special knowledges and skills to this enterprise.

It should be clear that civic science cannot be simply a device through which citizens are enrolled as helpers in a scientific process. As the Montana Study examples so clearly show, self governance rests upon civic processes of inquiry as well as action. In other words, civic science is not simply citizens doing the procedures of science with the help of scientists. Rather, **civic science involves scientists as citizens and citizens as lay scientists** in a process in which knowledge production is integrated with and therefore cannot be separated from the enlightenment function of self discovery and the moral effects of political deliberation and choice. In doing civic science neither traditionally scientific or traditionally civic ways of creating knowledge are privileged. Rather, these two knowledge systems and ways of thinking about the world interrogate each other in a process that leads to integration and more robust and meaningful knowledge.

In the case of forests, wildlife, water, and other natural resources, citizens can be vital participants in the investigation of questions regarding habitat requirements, history of land use, patterns of water flow, and so forth. This knowledge of experience is often missing from the work of research scientists, even when they seek to reconstruct the historical patterns of landscape processes. For example, when scientists were seeking to establish the historical levels of large woody debris in the creeks and streams of the Pacific Northwest, they extrapolated from the quantities observed in areas unlogged or otherwise seemingly unaffected by extractive management practices. At one meeting out in the woods with various local people, a veteran woods worker, listening to the scientists efforts to reconstruct these earlier conditions, burst out laughing as he recalled the efforts during World War II to provide cedar for the batteries powering the engines in planes, vehicles, and ships. He talked of running large bulldozers up nearly every drainage across the region and pulling out all of the fallen cedar trees! The scientists were amazed and quickly revised their assumptions regarding "natural" amounts of down trees along streams and in riparian areas in the Pacific Northwest.

Civic Science Is Part of the Life of a Community

Such examples illustrate that science can be improved if it is a part of the civic life of a society. Imagine what might have happened if the scientists had begun their work in the communities and had worked from jointly conceived problems! **Civic science locates the work of science within the community and makes it a part of the regular and necessary life of the community.** In the example above, the policy questions could move from simply narrowly defined biological problems, toward more broadly conceived problems located in history, past practice, and the dilemmas of past choices for today's problems. When problems are conceived in broad social context, the past cannot be so easily separated from the present. Thus, the question is not simply "what should be done about streams which are loosing their capacity to support healthy populations of fish?" but might also include "what social and political choices have led to this problem and why did they?" By asking these kinds of questions, citizens and scientists can address not only what to do about an immediate problem, but can also begin to develop ideas about how to address larger forces which affect their lives in more pervasive ways.

In civic science, citizens and scientists can learn from each other and help to mutually define problems, develop approaches to dealing with them, and hopefully learn something about themselves, each other, and their social and natural worlds. In a modern democratic society, citizens are necessary participants in science, not merely the subjects of scientific study or the passive recipients of scientific solutions. Active citizenship requires that citizens be engaged in creating knowledge, including scientific knowledge, in order to better imagine possible solutions and put them to work.

They had experienced the thrill of seeing action grow from their aspirations. By the democratic process of people with conflicting opinions sitting down together to study life in their own community, they had become better Americans—more tolerant, more understanding. They had learned how to free themselves from emotional prejudices that grow from political controversy. (Poston 1950:101).

The participation of scientists and citizens in a civic science process is an attempt to remove the constraints and tunnel vision that the specialization of roles produces. When science is no longer the exclusive domain of certified specialists, it begins to take account of the wider context in which it lives. In this way it can become more accurate in the advancement of knowledge as the commitment of science, and more meaningful to the improvement of society as the commitment of modern democracy. It is also fun for all involved.

The Conrad Study Group had generated such enthusiasm for community analysis that they decided to continue as a public forum. "Our country is in a dangerous state," said Mr. Christopher, district manager for the gas utility, "because our destiny is too often governed by pressure groups. A group like ours is a bulwark against that danger."

And besides that, it had been fun.

"We couldn't even bear to recess for the Christmas holidays," said Clara Withee (Poston 1950:101).

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Book Reviews

Forest Ecosystems

David A. Perry, 1994, Johns Hopkins University Press. (Cloth, $80.00; Paper, $49.95).

In both title and content, *Forest Ecosystems* reveals the importance of change in forestry. Thirty years ago a textbook in forest ecology would have been about trees, with a supporting cast of soils and climate (the defining "substrates" of trees), tree diseases and pests, and sometimes a concluding chapter on wildlife (that is, game but not nongame and fish). Perry's forest is not only trees; it is a complex and integrated ecosystem that occupies a broader landscape. In *Forest Ecosystems*, Perry is innovative in presenting basic concepts, creative in defining the connections among them, and thoughtful in choosing examples.

Traditional forestry, like large-scale industrial agriculture, deals "with the bewildering complexity of nature by eliminating it, by homogenizing forests to focus on a single crop" (p. xiii). The consequences of that approach are mined forest landscapes; degraded water resources; and, in the Pacific Northwest, depleted salmon stocks and unprecedented social upheaval and political controversy. Perry transcends that tradition and deals with trees *and* the complex ecosystems that they live in and depend on. He knows that human society depends on forests for a sustained supply of wood products—and also for numerous other goods and services; he strives to help everyone grasp both realities.

In 23 chapters, *Forest Ecosystems* shows that forests are complex systems with many interacting parts sustaining one another. One cannot understand the whole without understanding the parts. But neither can one maximize the production of any one part without protecting the other parts that enable that one to flourish. Three chapters establish this conceptual framework: the first overviews the book and reviews the state of world forests; the second defines *ecosystem* and other key concepts; and the third examines the role of forests in the global ecosystem (e.g., heat balance, carbon storage, water cycling, soil stabilization).

Perry visits forests via an "ecoscope," a magical device powered by imagination that allows one to travel back and forth in space or time. Readers learn that forests grow in more or less continuous bands circling the globe in the tropics and the Northern Hemisphere (about 35° N) but not in the Southern Hemisphere because of the lack of land masses. Broad climate patterns define these areas and the type of forests that occupy them; climate combines with topography, soils, disturbance, and the interactions of species to determine regional forest types and their distribution. Transects across the Big Horn Mountains of Wyoming and the Andes of South America illustrate variation in forests across gradients of these factors. But, as illustrated by acacia forest in Botswana, these patterns are dynamic: drought, grazing mammals (elephants), and disease interact to modify forest distributions in time. When supplemented with analysis of forest patterns in South Africa and Australia and from Alaska to Arizona, Tennessee, and North Carolina, the result presents a distinctly global perspective.

Turning from the landscape to local ecosystems, Perry introduces the reader to forest structure and dynamics. Traditional concepts—such as habitat, niche, food web, the self-thinning rule, soils, genetics, coevolution—are presented in new, more integrative ways. Readers learn how biological diversity is created and maintained. They learn how animals, microorganisms, and fungi, including mycorrhizae—the mutualisms between plant roots and fungi—are all critically important to forest ecosystems and landscapes. They learn about the soil system, its formation, structure, and influence on ecosystem processes.

Readers will learn still more. Productivity—the accrual of matter and energy in biomass—depends on the availability of nutrients, on climate, and the canopy structure of trees that must compete for light as they exchange gases with the atmosphere. Mixed-species stands can be more productive than monocultures because they are more stable against climatic fluctuations and other stresses, and they are better able to use available resources without competition.

Perry describes how pollution and management-related degradation threaten the species, structural, and process stability of forest ecosystems. Forest managers should, for example, see outbreaks of herbivores that threaten wood supply as signs of a coevolutionary breakdown, a failure to maintain the overall health of forests, not just trees. The consequences of breaking the links between plants and soils are singled our for detailed discussion as is the importance of protecting biodiversity for its stabilizing role in ecosystem protection. In this section of the book as elsewhere, a holistic view demonstrates how we can avoid or minimize those threats, and why it is important to do so.

From the nutrition of individual trees to the biogeochemical cycles that influence forest productivity and the global atmosphere, we must understand forests if we are to understand and perhaps even direct the future of human society. Trees and forests persist on Earth because they retain and release nutrients in ways that sustain forests; trees that did not "behave" this way are extinct. But global human activity is altering this interplay; forest landscapes are losing essential nutrients while soils are depleted and the atmosphere changes. The effects on forests, including perhaps reduced effectiveness of forest recovery mechanisms evolved over millions of years, can be seen locally and over broad geographic areas.

Throughout the text the reader sees not only trees but forests and forest landscapes and how their condition may damp or propagate disturbance within ecosystems and across the earth. Strategies to conserve species are thus not antithetical to logging but essential to the long-term maintenance of a timber industry.

More than any similar textbook I have seen, Perry merges practical forest management with lessons of conservation biology and basic ecology to create a forestry that comprises the entirety of things.

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Mountains and Plains—The Ecology of Wyoming Landscapes

Dennis H. Knight, 1995, Yale University Press, $40

The ecosystems and landscapes of western North America encompass phenomenal diversity of geology, plants, and animals, and landscape diversity has been very dynamic over time scales from years to millions of years. Getting to know any piece of these landscapes can be a lifelong endeavor. Dennis Knight has distilled decades of learning about Wyoming landscapes into this wonderful book that combines the best of ecology and natural history.

This tour of Wyoming begins with 3 chapters on the context for the development of ecosystems. The geography and plant communities are laid out in a very general way, along with simple descriptions of how ecosystems function. Landscape history charts the changes in Wyoming's relations with the drifting continents, through periods of uplift and erosion, and changes in climate and life forms. Approaching the present, Knight describes changes in climate, geology and glaciation during the Pleistocene and Holocene, and the modern-day implications for plant and animal communities. The key theme of these sections is that the land comprising Wyoming developed under a diverse set of conditions, and this history helps shape the current ecosystems of Wyoming in fundamental ways. Variations in landforms and elevation lead to wide ranges of climatic conditions in modern Wyoming, including precipitation ranging from 150 to 1500 mm/yr, frost free periods ranging from 0 to 50 days, and periods of growing-season drought from 0 to 5 months/yr.

After setting this stage, 9 chapters describe the environment, composition, dynamics, and land use history of major landscapes: riparian ecosystems, grasslands, sagebrush steppes, shrublands and playas, sand dunes and badlands, foothills and escarpments, mountain forests, mountain meadows, and alpine treeline and tundra. The coverage of each of these major landscapes is comprehensive and well-balanced. Knight is particularly careful to avoid unwarranted generalizations. For example, rather than paint pre-European riparian landscapes with a single broad brush, he notes that some large rivers (such as parts of the Bighorn River) had abundant floodplain forests, whereas others were devoid of trees (such as portions of the Sweetwater and Laramie Rivers). The impacts of beaver extirpation, cattle grazing, and water impoundments are summarized well.

Knight's ecology goes beyond the natural-history descriptions of ecosystem composition and structure to include substantial information on ecosystem function, including energy flow, nutrient cycling, and relationships between climate and productivity. Undue generalizations are again avoided; throughout the book a subtheme might be "local details matter." For example, one passage acknowledges that variations in time and space may be more important than averages: "Primary productivity and other aspects of ecosystem activity are often episodic, with pulses of plant growth, decomposition, and nutrient transfers occurring after rainfall events. Moreover, because the convectional rainfall of grasslands is oftan patchy, the amount of productivity and available biomass varies from place to place as well." Knight's interpretations of the ecology of landscapes achieves a clear image without sacrificing detail for simplicity.

Several areas of Wyoming warrant special consideration for ecological or historical reasons, and a chapters are devoted to the Yellowstone Plateau, Jackson Hole and the Tetons, and the Black Hills and Devil's tower. Key features of the Yellowstone chapter include fire history (and the landscape mosiac produced by interactions of vegetation, landform, and weather), and the impacts of large ungulates on willow and aspen vegetation. Some scientists insist that current use of winter range on the plateau by elk has led to unprecedented declines in willow and aspen communities, whereas others conclude the evidence is inconclusive or shows the results of natural dynamics across time periods of centuries. Although readers may wish to know which story is "true," Knight avoids taking sides and strives instead to present the conflicting views in a clear, informative way.

I hope this book will stimulate scholars to prepare books that examine the landscapes of other territories in western North America, and that they will be done with the thoroughness, balance, and style makes this book so informative and fun.

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Guide to the Birds of Alaska

Robert H. Armstrong, Alaska Northwest Books, $24.95

Field guides to birds likely outnumber field guides to all other animal taxa combined—as watchers of birds most assuredly far outnumber the sum total watchers of mites, insects, fishes, amphibians, reptiles, and other taxa. The proliferation of new, ever more geographically-restricted birding books aimed specifically at the traveling birdwatcher is a now well- established phenomenon. The strength of such books is the information pertaining to specific localities (where to see species x in state or province y), specific habitat associations wherein species x is most likely to occur, and some idea of relative probability-of-encounter for each species. Detailed information on species identification and how to differentiate unambiguously among similar species generally is not their strong suit. In the quest to be self-contained and complete as identification guides, many of these books are replete with inadequate and redundant information that is provided in more detail and with fewer errors in the major field guides of greater geographic scope.

Robert Armstrong's *Guide to the Birds of Alaska,* which first appeared in 1980, is one of the best established of the regional- guide genre, and now appears in a redesigned fourth edition. The book provides photographic and textual identification for 295 species that occur regularly in Alaska, and includes a lengthy supplemental list of casual and accidental species. Most featured species occupy a full page with one or two (occasionally three or four) photographs, and accompanying text divided into brief sections delineating field marks, similar species, and habitats. Many species accounts also provide a qualitative description of voice, and a very few give brief descriptions of behavior that may be helpful in distinguishing among species. Each account also contains a small status and distribution chart showing seasonal occurrence and qualitative relative abundance across six biogeographic regions into which the state is divided.

Many features differentiate this edition from the previous one, such as the considerable reduction in size that makes the new version more compact for ease of transport in the field. Nearly all of the photos in this edition are new and the quality of their reproduction is improved and more uniform compared with the third edition, in which species were illustrated with a mix of photographs, drawings, and paintings. Using only photos in the new edition imparts a more even quality to the book as a whole. The addition of a "similar species" component to each species account is a useful improvement, as is the more streamlined status and distribution chart.

Not all of the changes represent improvements. The third edition provided full species accounts and illustrations for nearly 100 Asian and Eurasian species of casual occurrence, and relegated only the extremely rare "accidentals" to a supplementary list in the rear of the book. For an advanced birder or professional field biologist making a trip to Alaska, the full inclusion of these species was the key reason for taking this book along (in addition to *The Birder's Handbook* and a National Geographic or Peterson guide). The most severe shortcoming of the new edition is the relegation of these species to a list that provides no more than a few identification hints and an indication of the bioregions where recorded previously. This problem is further compounded by omitting any mention of these birds (with few exceptions) in the primary accounts of similar species with which they might be confused.

Is there enough new information on habitat associations and status/distribution to have warranted a new, updated edition? In a random sample (n = 25) of species (but stratified to ensure breadth of representation across families), I found no changes in habitat information between the third and fourth editions, and minor changes in the status/distribution charts for only about 25% of the sampled species.

Given the apparent lack of much new information compared with the previous edition, I would guess that production of this new edition was not prompted by the need to revise the text in light of new data. The fourth edition is attractively produced, relatively compact, and has a nice overall "feel" to it. This redesign, combined with demotion of the casuals to a supplementary list, deletion of scientific nomenclature from the index, and inclusion of differentiating identification aids in the main species accounts, indicate to me that the primary impetus for this new edition was to simplify its content and thus increase its appeal

and (perhaps) utility for novice birders traveling to Alaska.

Although the book is attractive, and the non-technical, jargon-free text is written competently, I am left with reservations about its actual usefulness, especially for a novice birder. I am not a fan of using photographs as illustrations in identification guides. Although photos can have the advantage of imparting a more accurate gestalt of the bird, they rarely are superior to a competent illustration for highlighting physical characteristics that serve to differentiate among similar species. This viewpoint also was shared by the author in his Introduction to the third edition, wherein he suggested that "...the reader may also want to use, in conjunction with this book, one of the other field guides on the market when attempting to identify birds in the field." Unfortunately, this sound advice is nowhere to be found in the new edition.

Nearly half of the photographs in the fourth edition were taken by the author, and display well his fine eye as a photographer of birds (many of the rest derive from the VIREO collection at the Academy of Natural Sciences in Philadelphia). Photos were "...selected to show field marks, not simply a pretty pose," and many succeed in this endeavor. Not surprisingly though, some species lack photos that adequately illustrate the key differentiating characteristics, and thus will be of little help to a truly novice birder. This problem also produces some disconnects between the text description of field marks and the selected photographs. For example, the key characteristic that will unambiguously differentiate the Three-toed Woodpecker from the Hairy or Downy Woodpeckers is the "Dull black-and-white- barred back" of the former and the "unmarked white back" of the latter two species. The accompanying photograph of the Three- toed Woodpecker, however, appears to be of the Rocky Mountain form (subspecies dorsalis), in which the back is essentially unmarked and entirely white.

There are some minor production problems, as well. In general, the color balance of the reproduced photographs is quite good, aside from a few notable exceptions like the drake Mallard with a purple (instead of green) head. The most egregious mistake is the photograph of a Green-backed Heron (which occurs only as an accidental in Alaska) to illustrate the American Bittern account! The quality of the binding poses a more serious problem that may deter some from purchasing this book. The publisher states on the jacket that the new edition bears a "Durable lie-flat binding, for all-weather field use." It is true that the sewn binding of the previous edition did not allow it to lie flat, while the glued binding of the new edition does. Simply turning the pages of my copy (indoors, sans rain, snow, or wind), however, already has caused several pages to begin detaching from the binding. Having experienced firsthand the travails of trying to convince publishers of the necessity for a sewn or otherwise truly durable binding for a field guide, I can only speculate that the publisher's decision to change from a sewn (i.e., more expensive) to a glued binding may have been driven by short-sighted economic considerations.

In the new edition, Armstrong has added two introductory paragraphs concerning the conservation of Alaska's birds. This is a welcome, but much too brief, addition. Given the crisis in conservation that we face today, it is imperative that authors of field guides take advantage of the opportunity provided to heighten awareness and educate their readers -- especially in a book destined for both general public and professional audiences.

This new edition is attractive, and it is a good guide both to species distribution and to probability of encounter with the regularly occurring birds of Alaska. For myself, I probably would not purchase the new edition if going to Alaska, especially if I already had the third edition. I would, however, recommend this book to a novice or less-than-fully-competent birdwatcher traveling to Alaska, but only with the caveat that it be used in conjunction with their National Geographic or Peterson identification guide.

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A Primer of Conservation Biology

Richard B. Primack, 1995, Sinauer Associates Inc., Sunderland, MA. 277 pages (paper $18.95).

Essentials of Conservation Biology is an excellent textbook to introduce undergraduates to the breadth of the emerging discipline of Conservation Biology. Since first reading it, I have felt that *Essentials* is a book that should be required reading for every college student; it is certainly as important as the essentials of mathematics, chemistry or English, and perhaps more critical to the long-term health of natural communities on our planet.

I could hardly be any less favorably inclined to recommend *A Primer of Conservation Biology*; it is essentially the same book, albeit a condensed version with a different cover, table of contents and price. At first glance *A Primer* appears to be considerably less than *Essentials*, but although the table of contents has far fewer entries (there are 5 chapters as opposed to the original five parts and 22 chapters), but the new chapters basically equate to the "parts" of the original work. The changes, if any, are more hierarchical than anything else; most of the topics covered in the original work are also covered in *A Primer*, simply at a different level of heading.

A Primer is an excellent introductory text; however, I have questions pertaining to who its target audience might be. From my perspective as a college teacher, *Essentials* is presently the ideal introductory conservation biology text for students majoring in the biological and natural resource sciences. I should add that it is also suitable for non-major students enrolling in those same classes. *A Primer* would logically have been written for all those other students in the university who don't enroll in the courses just alluded to as well as interested lay readers. I surely hope that such courses will be available in these times of budget crises and retrenchment among universities. The author states in the preface that *A Primer* was written to "provide a brief but thorough introduction to the major concepts and problems of the field." To that statement I question why he eliminated the 35 boxes that illustrate so well the real-life problems of conservation biology. These case-histories are probably the best tool for translating theory and principle into real-world situations. I would suggest that *A Primer* is much less than it would have been had those boxes been retained. Importantly, the illustrations are excellent and mostly make clear points that beginning students will easily grasp.

No honest book review could be complete without criticism, and here I will try to establish my honesty. Any work purporting to cover the field of conservation biology requires a far more extensive and intensive section on invasive alien species and their role in species loss and community perturbation. I consider *A Primer*'s coverage of this topic terribly anemic. In a similar vein, the oceans cover three-fourths of our planet and provide humans with one-fourth of our annual protein consumption. Nearly every commercial species has dramatically declined, often dangerously so. We continue to discharge huge quantities of poisons into our oceans. This is not a topic to be treated either lightly or briefly, yet for example, the topic of commercial fisheries is skimmed over in less than 2 pages. The author is not alone among terrestrial ecologists in failing to adequately deal with marine problems, nevertheless the treatment is inadequate.

At times it seems that there could be better connectivity among sections and topics. For example, in the section of Extinction Rates On Islands (page 61) it might have been pointed out that while indeed extinction has been mostly an island phenomenon for the past 400 years or so, more importantly it is largely due to exotic organisms (finally mentioned weakly on page 95). In the case of Madagascar (also mentioned on page 61) the current extinction event is a direct outgrowth of human colonization and land-use, a topic covered in the preceding section, but not referred to in the subsequent discussion.

The author makes an occasional unfounded or misleading statement. For example, on page 91 a photo of a fur buyer and his large pile of raccoon pelts is accompanied by a caption that states that "such over harvesting by trappers imperils many other species ..." This would have been better presented if those imperiled species were documented. The illustration stands as an indictment of trapping, yet no proof was offered that trapping indeed imperils furbearing species. At least in North America, no species is currently imperiled by trapping, although a few are still absent from portions of their former range as a result of historical trapping. Additionally, the

picture seems to make a statement about raccoons as well (admittedly the caption states that raccoons are not currently at risk); since the raccoon is a highly irruptive species that mostly needs to be concerned with the distemper virus and high-speed vehicular traffic, this photo might have been a misleading, dramatic way to make a point. There is enough controversy and surely enough environmental concerns in conservation biology without having to resort to misleading readers.

Nevertheless, *A Primer of Conservation Biology* is an excellent condensation of *Essentials*. Although its length and bibliography are roughly half of the original work, I noticed that a number of references had been published since. Apparently the author has been revising and condensing simultaneously. I applaud the effort.

All criticisms aside, I enthusiastically recommend *A Primer of Conservation Biology* although I am not entirely certain at this moment who I am recommending it for. At its very reasonable price it might be an additional book assigned to any number of courses and might serve well in that role. If there are service courses for students outside of the biological and natural resource disciplines, this book would be ideal for them. My guess is that it will seek its own niche among students and courses not targeted at biology/natural resource majors. Certainly, if every student was required to read this book the world would eventually be a better place for all species.

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From Coastal Wilderness to Fruited Plain: A History of Environmental Change in Temperate North America From 1500 to the Present

Gordon G. Whitney, 1994, Cambridge University Press, New York

In this era of public land management efforts to understand historic patterns of variation in ecosystems, *From Coastal Wilderness to Fruited Plain* very patiently presents historical accounts of evolving human effects on ecosystems of the Northeast and Upper Midwest of the United States. Even the uninformed reader is immediately lured into the book's historical reflection upon humankind when a look at the table of contents reveals chapter titles like "The forest primeval," "Assault upon the forest," (with follow-up chapters on the farmer, the lumber industry, and fuelwood), "Predatory agriculture," "An impoverished fauna," and "The legislated landscape." These titles, and the emotional analysis of human behavior and values implied, immediately fuel hungers for understanding how we fit into the landscape we currently know.

The overwhelming number of historic narratives that Dr. Whitney has reviewed and woven into this tale of transition of the Eastern North American landscape provides a capturing story. You probably will not be able to take it in all at one setting, however. The hundreds (thousands?) of citations (105 pages of references!) slightly interfere with total immersion into the story itself. One often stops to ponder the name or the date of the references used to emphasize each point made. It is the kind of book that is better read by just picking it up and reading a few paragraphs or a few pages, either in sequence, or wherever it happens to open. It may also be very useful as a reference source when specific questions arise.

Dr. Whitney attributes the opportunity to compile such a historical analysis to time spent on a sabbatical at Yale in the School of Forestry and Environmental Studies. This says a lot for sabbaticals. As one reads the accounts of early settlers, surveyors, botanists and timber workers, it is not difficult to imagine Dr. Whitney searching over historical narratives and survey details, making notes, becoming excited about the images that were developing and plans for how to tie them together in this narrative. One can only imagine the time it takes to find, read, synthesize and tell the stories contained in these historical sources.

The book begins with a fifteen page "photographic essay" which is intended to illustrate the character and the demise of the presettlement vegetation of the Northeast and Midwest. Old pictures of big trees and woodsmen always interest this reader, but these pictures are suspended from the book, without the contextual explanations to make them meaningful. They seem to be random photos of random places at random times. White pine and yellow birch in Connecticut, red spruce and hemlock in New Hampshire, maple in Michigan, yellow poplar in Indiana, white oak in West Virginia and prairie dock in a sea of tallgrass prairie in Wisconsin are interesting, but have no context at this point. Closing the book with this creative idea of a photographic essay, once the reader has the historical context, would be much better.

Quite early in his discussion of methods used to restructure the past, Dr. Whitney successfully introduces the reader to the emotional excitement of historical ecology with a quote by Ralph Waldo Emerson in 1836: "All the facts in natural history, taken by themselves, have no value, but are barren, like a single sex. But marry it to human history, and it is full of life." This is the purpose of the book, to speak to the natural and social sciences, blending ecology with an understanding of human behaviors and values.

Dr. Whitney (through Emerson) provides the incentive to struggle through the detailed accounts of timber, agriculture and development pressure on the United States landscape in an effort to find out what happened to the pristine places noted by early European settlers. Dr. Whitney impresses upon the reader the importance of understanding the relationship between landscapes and the societies that shape them. To do this, he presents the culture from which the early American colonist emerged. A review of timber utilization patterns and agrarian practices in Europe provides context for the impacts of the dominant culture of American settlers. Then, with context established, we understand the stories of the American farmer better: "In the settlement and the civilization of the country, bread more than timber or beauty was wanted" (Muir). From discussions of techniques and immediate impacts of clearing

forest to a discussion of the common farming practice of "grazing out the woods," Dr. Whitney presents only the historical accounts of what happened and how the landscape was influenced; the reader easily begins to actively imagine how he or she would have reacted to the massive changes this society experienced.

Next came the lumber industry. With post-Civil War expansion and rapid technological advancement, lumbering advanced from highly selective white pine harvesting to focus on secondary species. Dr. Whitney's stories of Maine, Pennsylvania and Michigan are stories of people, of towns, of relationships with the land. Not only the landscape was changing, but technology demands, jobs, wildlife, and society were changing with it. The accompanying changes from an abundance of fuelwood (some families of the 18th century are believed to have used as much as 60 cords of firewood in one year) to some level of scarcity to a switch to dependence on alternative fuels also impacted the landscape and daily lives of people.

In 1889, the American farmer was accused of gross vandalism of the land in the way it was managed. Whitney chose to describe the American system of farming as predatory agriculture in a chapter by that name. In defense of the farmer, however, he does acknowledge that the dominant theme in agricultural change has been constant adjustment to new economic conditions and forces. Trial and error was often the method of learning.

From Coastal Wilderness to Fruited Plain winds down with lengthy discussions of forces and effects related to introduction of exotic vegetation and changes in wildlife populations. Logging, forest fragmentation, intensive farming and urban development had vast effects on all aspects of the landscape. As the United States transitioned to a more regulated landscape by the mid-twentieth century, there was promise in the development of a new ethic for its management, with greater understanding of the extent of human influence on that landscape.

We seem at a crossroads in science at the present time. Our leaders, and the public, are demanding more integrated analysis of the effects of our land management practices. We are not a stable population. Much as our cities have grown and taken shape from our countryside, the urban residents there are now descending upon our remaining rural areas, for recreation, second home purchases and for retirement. Where we once described ourselves as a pioneering society, bent on extractive relationships with the forests and grasslands, we have moved to a society of great demands on natural resources to support a grand life style, but our land ethic has become instilled in policy and legislation; our residents have acquired great appreciative value for places where the forces Dr. Whitney discusses have had the least influence. Dr. Whitney closes with some degree of optimism: "We cannot predict the outcome of every human action, but we can use our knowledge of environmental change in the past to create a better future - a future that respects the land and its ecological contraints."

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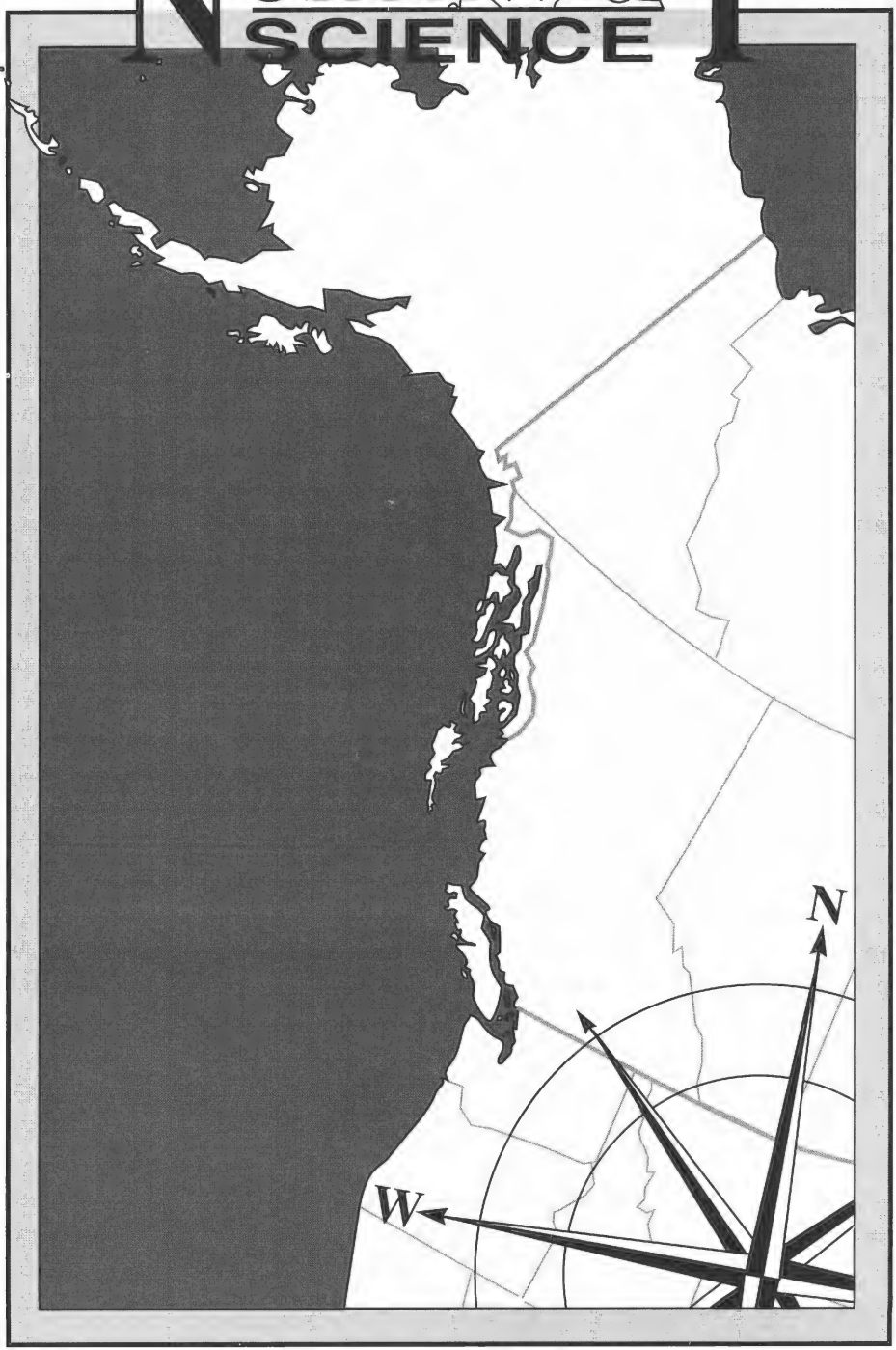

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Announcements

1996 Honorary Life Member Award

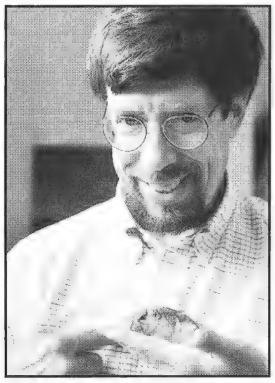
The Honorary Life Member award is normally given to a scientist who has made a significant contribution to the Northwest Scientific Association. The Association breaks with that tradition this year, and recognizes someone who is not a scientist but has made a unique contribution.

Northwest Science is the official journal of the Association. It arrives in offices and libraries throughout North America four times a year. The Editor is responsible for providing reviews of manuscripts, but after final copy leaves the Editor's desk, it is sent to the Managing Editor who turns a mixture of text, tables, figures, and electronic copy into a polished, professional-looking issue of the journal.

That Managing Editor is Nancy J. Grunewald. Nancy is journals coordinator for Washington State University Press, where her work includes serving as production editor, subscription manager, and editorial liaison for no less than six journals, one of which is *Northwest Science*.

After earning a bachelor's degree in music at WSU, Nancy began working at WSU Press in 1977, in the days of magnetic tape word processing. Through the years of changing technology, she mastered phototypesetting and more recently, desktop publishing systems. Her relationship with *Northwest Science* began in 1983 as a typesetter. More responsibilities were added over the years until today she oversees the journal's production, subscriptions, and budget.

In describing Nancy, professional is the first word that comes to mind, followed by meticulous, dedicated, hard-working, friendly, and patient. Despite her many responsibilities (including training the present Editor), she maintains an amazingly upbeat attitude. As Managing Editor, she provides the continuity to sustain the publishing process through editorial and board changes. The Northwest Scientific Association is pleased to acknowledge her 13 years of outstanding service to *Northwest Science* and her efforts on behalf of the Association. We proudly recognize her as our newest Honorary Life Member.



1996 Outstanding Scientist Award

The Northwest Scientific Association has named Dr. Charles J. Krebs as Outstanding Scientist for 1996.

Charles Krebs is a population ecologist at the Department of Zoology of the University of British Columbia. He has studied population cycles of lemmings, voles, and snowshoe hares in northern Canada for the last 37 years, and has pioneered the field experimental approach to population dynamics. He obtained his bachelor's degree in wildlife management at the University of Minnesota and his masters and Ph.D. at the University of British Columbia under Dr. Ian McTaggart Cowan and Dr. Dennis Chitty. After a Miller Postdoctoral Fellowship at the University of California, Berkeley, with Dr. Frank Pitelka, he moved to Indiana University in Bloomington where he taught for 6 years and first described the "fence effect" in field vole populations.

In 1970 he returned to British Columbia and began a series of studies in field voles, lemmings, and snowshoe hares in the Yukon and Northwest Territories. From 1982-84 he was Chief of the Division of Wildlife Research of CSIRO in Australia. In addition to his research, he has published three ecology textbooks: *Ecology* (now in its 4th edition), *The Message of Ecology,* and *Ecological Methodology*. Dr. Krebs is a Fellow of the Royal Society of Canada and was awarded an honorary D.Sc. by Lund University in Sweden. For the past 10 years he has been the director of the Kluane Boreal Forest Ecosystem Project in the Yukon.

(*Announcements continued on next page.*)

Minutes of the Northwest Scientific Association Board of Trustees Meeting Tacoma, Washington, 20 March 1996

Highlights

1. President Jan Henderson introduced Richard Cellarius, Director of the Graduate Program in Environmental Studies at the The Evergreen State College, Olympia, Washington. Dr. Cellarius will serve as President of NSA when the annual meeting is held at Evergreen State College in 1998.

2. Treasurer's Report. NSA Treasurer David Hansen reported a net loss of $10 for fiscal year 1995. Current NSA membership is 427 members. *Northwest Science* Managing Editor Nancy Grunewald noted that subscription revenues declined, while expenses for postage and handling were all higher in 1995.

3. Editor's Report. *Northwest Science* Editor David Peterson indicated that submission of manuscripts to the journal during 1995 were about 20% higher than in 1994. Acceptance rate is 50%, rejection 30%, withdrawn or failed to submit a revision 20%. Two special issues have been submitted and are being prepared for publication. Special issues are an increasing burden on limited editorial staff and incur costs beyond normal page charges. This concern will be addressed by a committee that will develop a policy on submission of special issues and appropriate publication charges.

4. Honors and Awards Committee Report. Michael Pitt reported that the committee had accepted the nomination of Charles Krebs, Department of Zoology, University of British Columbia for Outstanding Scientist for 1996.

5. Student Awards Committee Report. Jerry Wolff reported that the committee received 13 proposals from eight institutions. Four proposals were selected for grants of $400 each.

6. 1997 Meeting Plans. Robert Carr indicated that the 1997 meeting would probably take place 28-31 March. Eastern Washington University is hosting the meeting, which will be held off-campus in Spokane, Washington. Ross Black of EWU will serve as senior program director for the meeting. Several symposium topics have already been suggested, and the meeting will include other professional societies.

(A complete list of the minutes is maintained in the files of NSA Secretary Denis Lavender.)

1996 Student Research Grants

Each year the Northwest Scientific Association conducts a student research proposal competition. Small monetary awards are provided to support student research projects at colleges throughou;the Northwest. Funds for this activity come from member contributions to the Associations research fund.

Four winners were announced at the 1996 meeting of the Association in Tacoma, Washington, with each student receiving a $400 grant. The winners and their research topics are:

- **Deborah Buetler,** Washington State University—Local and landscape factors influencing the distribution of brown-headed cowbirds in managed forests of northeastern Washington
- **Robert Drew,** Washington State University—The impact of introductions on phylogeographic patterns of *Martes pennanti* ($400)
- **Jason Thomas,** Washington State University—Developing a spatially-explicit population simulation model for snowshoe hares in northeast Washington ($400)
- **Robert Wagy,** Oregon State University—The phenotypic correlates of reproductive success in the gray-tailed vole, *Microtus canicaudus* ($400)

Deborah C. Strohmeyer,[1] and **James M. Peek,** Department of Fisheries and Wildlife, University of Idaho, Moscow, Idaho 83844

Wapiti Home Range and Movement Patterns in a Sagebrush Desert

Abstract

Daily movement descriptions have not been available for wapiti (*Cervus elaphus*) using sagebrush (*Artemisia tridentata*) and cropland. Thus, we quantified home ranges and daily movement patterns of radio-collared wapiti in a sagebrush-cropland mosaic in southeastern Idaho. Wapiti in our study had the largest home-range sizes and traveled the longest daily distances of 14 and 8 investigations, respectively. Annual, minimum-convex-polygon home-range areas for nonmigratory wapiti in our study ranged from 544 to 555 km^2. Summer, minimum-convex-polygon home-range areas ranged from 79 to 593 km^2. Summer, harmonic-mean core areas ranged from 26 to 148 km^2. Mean-minimum-daily distance traveled by marked wapiti from June through August was 8.8 km (SE = 0.8, n = 59). Large home-range sizes have been correlated with low precipitation; however, juxtaposition of habitat components in our study area also contributed to long daily movements and large home-range areas. During the summer, daytime bedsites were in native rangeland, while nighttime relocations were in cropland. We speculate that the most important (interrelated) factors behind the large wapiti movements in the INEL area were aridity, juxtaposition of habitat components, habitat requirements, and human disturbance.

Introduction

North American wapiti management has been based largely on information collected in montane habitats. In light of wapiti range expansions in semi-arid habitats during the last 2 decades, information on ecology of wapiti in these areas is needed. Wapiti now occupy treeless habitats in the Red Desert in Wyoming, the Arid Lands Ecology Reserve in south-central Washington, the Idaho National Engineering Laboratory (INEL) in southeastern Idaho, and the Great Basin of south-central Oregon. Baseline biological information is needed by managers if non-montane wapiti populations are to be effectively managed. For example, understanding wapiti home-range patterns and movements is necessary for strategic harvest planning (Boyce 1989:13) and for effective handling of crop damage complaints.

Our data is important because movement and home-range information on wapiti in sagebrush-steppe has been rare. Plus, cropland use has not been reported for wapiti using sagebrush-steppe (McCorquodale et al. 1986, McCorquodale 1987, McCorquodale et al. 1989). Home-range descriptions have been available only from south-central Washington, which was at the northwestern edge of the sagebrush-steppe (McCorquodale et al. 1989). Depending upon information from one location may be problematic because there may be factors of interest that were different for that site. Our information complements data from south-central Washington because there were substantial differences in water availability and in sagebrush:grass biomass ratio between these 2 areas. The Washington site had a perennial stream, while surface water in the INEL area was limited to artificial sources, including irrigated cropland. The sagebrush:grass biomass ratio was lower in Washington.

Wapiti colonized the INEL area by the mid-1980s (Moritz 1988). This colonization coincided with increased water availability via Bureau of Land Management (BLM) guzzlers and severe winters. Two wapiti herds, each roughly 80 animals, had formed by 1989 (Strohmeyer 1992). Cropland damage complaints increased with wapiti numbers. Our objective was to describe home ranges and daily movements.

Study Area

The study area encompassed private, public, and INEL lands. Most of the private lands were cropland. Public lands included BLM, United States Forest Service, and state lands. The INEL covered 2,305 km^2 in southeastern Idaho and was established in the 1950s to test nuclear reactors. Public access was restricted while livestock grazing

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was limited to the INEL's periphery. Hunting on INEL land was limited to depredation hunts which extended 0.8 km inside the NE border in the Mud Lake area.

Elevations ranged 1454-1554 m (Harniss and West 1973). The rolling topography was broken by volcanic craters and cones. Precipitation peaked in December-January and May-June. From May 1989 to August 1991, mean annual precipitation was 20.3 cm, and mean July and January temperatures were 32.3 C and -1.6 C, respectively (R. Mitchell, U.S. Dep. of Energy., unpubl. data). Surface water was restricted to artificial sources: guzzlers, cropland irrigation, and waste-water ponds near INEL facilities.

Adjacent croplands were primarily alfalfa with some potato, wheat, barley, oats, and rapeseed. About 87% of the INEL was sagebrush-steppe, with the rest being grassland and juniper (*Juniperus* spp.) woodland (McBride et al. 1978). The juniper woodlands were concentrated in the Lemhi mountain foothills and the Cedar Butte Lava area. Common grasses were bluebunch wheatgrass (*Agropyron spicatum*), needle-and-thread (*Stipa comata*), and Indian ricegrass (*Oryzopsis hymenoides*).

Methods

Female and male wapiti were captured by helicopter net-gunning and each animal was radiocollared and ear-tagged. We relocated marked wapiti from April 1989 through August 1991, visually verifing relocations when possible. No more than 2 relocations were recorded every 24 hours per individual to minimize temporal dependence between relocations (Swihart and Slade 1985).

Diurnal aerial relocations were obtained from fixed-wing aircraft using Loran-C devices (Boer et al. 1989). Nocturnal, aerial relocations were made with a helicopter-mounted infrared system which allowed visual verification of wapiti. Accuracy of the Loran-C systems used were not tested, but Patric et al. (1988) found mean error in location accuracy for such devices to be 1.0 km (0.1 SE, $n = 18$).

We plotted ground relocations in Universal Transverse Mercator System (UTM) coordinates. Ground relocations were obtained weekly during winter and biweekly during summer (once diurnally, once nocturnally). Nocturnal telemetry work in winter was limited to weeks coinciding with a full moon. Croplands were surveyed for presence of wapiti during June when marked wapiti use was intermittent.

No triangulation errors occurred for ground, cropland relocations because marked animals were either seen or their nocturnal presence was verified by fresh tracks and feces. We estimated triangulation error for ground, non-cropland relocations by comparing triangulations to subsequent, corresponding visual relocations. We randomly selected 75 relocations that had both triangulation and visual information. We defined the error between a triangulation and respective visual relocation as the distance between the visual relocation and the center of the polygon formed by intersecting bearings. The mean of this distance was 0.3 km (0.04 SE, $n = 75$).

The harmonic--mean estimator in Program Home Range (Ackerman et al. 1990) best quantified our home-range areas. However, we also reported minimum-convex-polygon (MCP) areas because they have been the most commonly reported. We estimated seasonal home ranges for each marked wapiti having ≥20 relocations. Timing of migrations, changes in group sizes, and timing of cropland use led us to define seasons as: summer = July-September, fall = October-December, winter = January-March, and spring = April-June.

We quantified minimum-daily movement patterns during June, July, and August by calculating distances between consecutive daytime and nighttime relocations. Only relocations occurring <1 day apart were used. We defined daily distance, the distance moved in a 24-hour period, to be twice the respective day-night distance because a 24-hour period involved animals moving from shrub-steppe (day) to cropland (night) to shrub-steppe (day).

Statistical Analyses

A factorial analysis of variance tested differences among seasonal home-range areas and among daily distances. We tested pairwise comparisons with population marginal means because sample sizes were unequal (Searle, Speed, and Milliken 1980). Power calculations followed Desu and Raghavarao (1990:58-9). The 95% harmonic-mean areas were not transformed. A

natural logarithmic transformation normalized the MCP areas and the daily distances; however, we reported untransformed means and standard errors. The repeated measures (multiple relocations of marked individuals) in the daily distances were removed by using the mean distance for a given animal-month-year varied largely because of legal harvest of marked bulls. Marked wapiti were relocated 1403 times. Sixty-one percent of daytime, ground relocations and 88% of daytime, aerial relocations were visually verified. Cropland relocations totalled 356, of which 354 were verified either visually or with fresh wapiti fecal material and tracks.

Annual Home Ranges

Distribution of the Mud Lake-Argonne (MA) herd was almost exclusively on INEL land (Figure 1). This herd wintered in the central portion of INEL land near the Argonne facility then summered in the Mud Lake area. We consider these animals to be nonmigratory because their shifts in home-range use were gradual (>2 months) and

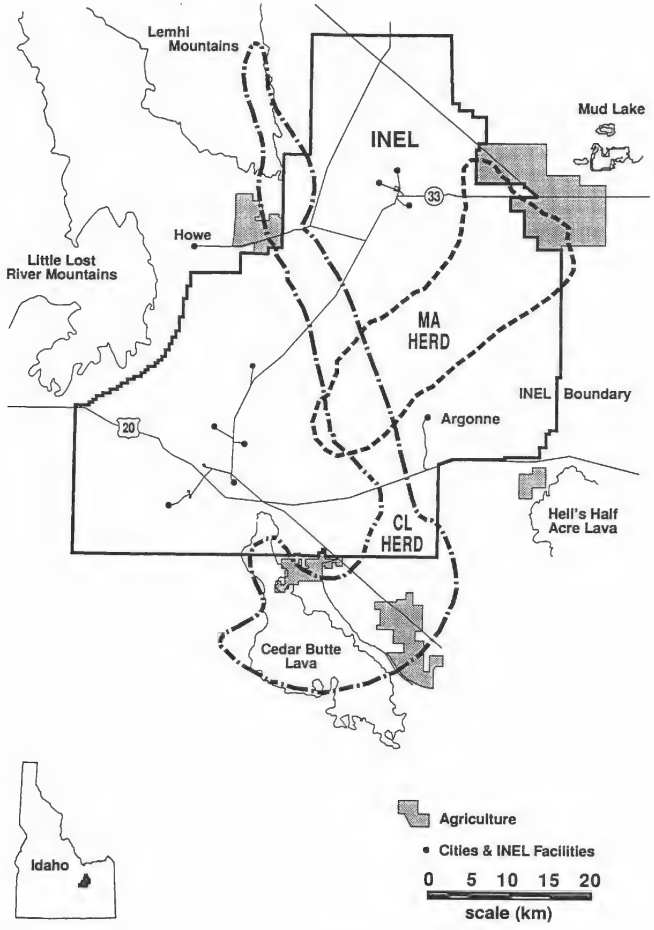

Figure 1. Annual Cedar-Lemhi (CL) and Mud Lake-Argonne (MA) wapiti herd distributions in the Idaho National Engineering Laboratory (INEL) area. Marked males having distributions that only partially overlapped with the cow-calf herds were not drawn.

the distance between their winter and summer areas was about 9 km. We calculated annual home-range areas for 3 MA wapiti (2 males, 1 female). For these areas, the number of relocations per individual ranged from 91 to 152. Their mean MCP area was 551 km^2 (3.6 SE, $n = 3$).

In contrast, the Cedar-Lemhi (CL) herd spent much of its time on non-INEL land, using the central portion of the INEL only when migrating between the wintering area, Lemhi mountains, and the summering area, Cedar-Butte-Lava area. Time spent by CL wapiti during migrations varied from 2 days (fall) to 3 weeks (spring). Annual home-range sizes for CL wapiti were not calculated because the distance between the edges of their summer and winter areas was about 40 km.

Seasonal Home Ranges

The number of calculable home-range areas for marked individuals varied with season (Table 1). No winter home-range sizes were calculated because the number of relocations per individual was <20 for all animals. The highest numbers of relocations per individual occurred in the summer. Twelve of the 14 summer home-range areas had >30 relocations/individual. All spring and fall home-range areas had ≤31 relocations/individual. Spring and fall home ranges for CL wapiti were awkward to quantify because movement between the Cedar Butte Lava area and the Lemhi Mountains occurred at these times. Fall home ranges of CL wapiti were especially troublesome because movement between the Cedar Butte Lava area and the Lemhi mountains occurred more than once for some animals and patterns of individuals were not consistent between years. Thus, spring and fall home ranges for CL wapiti refer to the area, either Lemhi Mountains or Cedar Butte Lava, where most of a given marked animal's time was spent.

The MCP home-range areas had interaction between seasons and herds ($F = 9.2$; 2, 16 df; $p = 0.002$). Fall, MA areas were the largest for all season-herd combinations ($p \leq 0.02$). Summer and spring areas were not different between herds ($p \geq 0.2$). Summer areas were larger ($p \leq 0.01$) than spring and fall areas for CL wapiti. The log transformation created asymmetrical confidence intervals causing variation in power. Thus, power for detecting a 50 km^2 (effective size) difference between 2 home-range areas, was about 0.2 at upper confidence interval boundaries and was 0.5-0.6 at lower confidence interval boundaries. Similarly, power for detecting a 100 km^2 difference between 2 areas varied from 0.5-0.6 to >0.9 at upper and lower confidence interval bounds, respectively.

Differences among the 95% harmonic-mean home-range areas were not significant ($F = 1.8$; 16 df; $p = 0.16$). This conclusion may be an error because power was low. Power for detecting a 50 km^2 difference (effective size) between 2 home-

TABLE 1. Seasonal home range size by herd, gender, and method for wapiti in the Idaho National Engineering Laboratory area, 1989-1991. Sample size was the number of individual wapiti.

Category	Sample size	Range (km^2)	Mean (km^2)	SE
Minimum Convex Polygon Home Range				
Mud Lake-Argonne				
fall	3	438-480	466	14
winter[a]	0	—	—	—
spring	2	143-198	170	28
summer	5	114-220	165	22
Cedar-Lemhi				
fall	3	65-116	91	15
winter[a]	0	—	—	—
spring	4	61-130	95	14
summer	9	79-593	245	55
95% Harmonic Mean Home Range				
Mud Lake-Argonne				
fall	3	246-274	257	9
winter[a]	0	—	—	—
spring	2	116-218	167	51
summer	5	47-479	335	78
Cedar-Lemhi				
fall	3	132-177	149	14
winter[a]	0	—	—	—
spring	4	115-250	170	31
summer	9	133-332	265	21
Harmonic Mean Core Area[b]				
Mud Lake-Argonne				
fall	3	0-105	57	31
winter[a]	0	—	—	—
spring	2	0- 0	0	0
summer	5	93-148	128	10
Cedar-Lemhi				
fall	3	41- 55	46	4
winter[a]	0	—	—	—
spring	4	0- 82	46	18
summer	9	26- 86	70	7

[a]Not quantified because number of relocations per individual <20.

[b]A 0.0 value for a core area indicates Program Home Range did not detect a core area for at least one individual.

range areas, was 0.25. Power for detecting a 100 km^2 difference between 2 areas was 0.73.

Harmonic-mean core areas had interaction between season and herd ($F = 6.9$; 2,16 df; $p = 0.007$). Summer core areas for MA wapiti were the largest ($p \leq 0.005$) for all herd-season combinations. Spring core areas for MA wapiti were smaller ($p = 0.04$) than their fall core areas. Spring core areas for MA wapiti were also smaller ($p = 0.01$) than summer core areas for CL wapiti. Power for detecting a 20 km^2 difference (effective size) between 2 core areas, was 0.5. Power for detecting a 35 km^2 difference between 2 core areas was 0.9.

Daily Distances

Spatial differences in wapiti movement patterns contributed to differences in daily distances traveled. CL males had home ranges that only partially overlapped with that of CL females. Home ranges of MA males overlapped with that of MA females, but MA males often moved independently of MA females. For example, infrared, helicopter scans of Mud Lake-area croplands in July showed MA wapiti, including some males, would be in 1 grain field while several all-male groups of 1-3 animals would be scattered across alfalfa fields.

Daily distances were different among herd-month-gender combinations ($F = 8.7$; 1,33 df; $p = 0.006$). Daily distances traveled by CL males increased ($p = 0.01$) from July to August (Table 2). Increases in daily distances traveled by MA females and MA males from June to August were not significant ($p \geq 0.2$). The decrease in daily distances traveled from July to August by CL females was also not significant ($p \geq 0.9$). Again, the log transformation created asymmetrical confidence intervals causing power to vary. Thus, power for detecting a 2.0 km difference (effective size) between two mean distances was 0.1 and 0.3 at upper and lower confidence boundaries, respectively. Power for detecting a 5.0 km difference between two mean distances was 0.5 and 0.8 at upper and lower confidence boundaries, respectively.

Cropland Use

Intermittent cropland use by marked wapiti began in June. Track surveys in the Mud Lake area showed wapiti used cropland nightly in groups of 5-10 animals. Track surveys in the Cedar Butte

TABLE 2. Daily distances by herd, month, and gender for wapiti during June-August in the Idaho National Engineering Laboratory area 1989-1991. Sample size was the number of unique animal-month-year combinations.

Category	Sample size	Mean (km)[b]	SE[c]
Overall	59	8.8	0.8
Herd-Month-Gender[a]			
CL-June-female	0	—	—
CL-June-male	0	—	—
CL-July-female	13	9.6	2.0
CL-July-male	3	8.4	4.1
CL-August-female	13	4.9	0.9
CL-August-male	4	17.3	3.3
MA-June-female	2	7.5	0.8
MA-June-male	1	4.4	—
MA-July-female	5	8.2	1.1
MA-July-male	7	9.1	1.0
MA-August-female	4	10.4	2.6
MA-August-male	7	10.2	1.2

[a]MA = Mud Lake-Argonne herd; CL = Cedar-Lemhi herd.

[b]— = No data available.

[c]— = Not calculable.

Lava area also showed nightly cropland use by wapiti. Marked wapiti from both herds exhibited a distinct circadian pattern from July through September. Daytime bedsites were in native rangeland, while nighttime relocations were in cropland. MA wapiti entered and exited cropland in darkness, while CL wapiti often entered cropland before sunset and exited after sunrise. No daytime cropland relocations for MA wapiti occurred, while CL wapiti were occasionally relocated in cropland during rainy days. Crops used by wapiti changed over the summer. Wheat, oats, and barley were crops used until the end of July when these crops were dried for harvest. Wapiti began using alfalfa at this time. Alfalfa use became intermittent in October, ceasing with freezing nighttime temperatures. Daytime and nighttime areas were generally the same for marked wapiti from October through May.

Discussion

Annual, MCP home-range sizes for MA wapiti, 551 km^2, were larger than that for other nonmigratory wapiti and red deer (*Cervus elaphus*) herds in non-arid environments which ranged 3-112 km^2 (Catt and Staines 1987, Craighead et al.

1973, Edge et al. 1985, Edge et al. 1986, Franklin et al. 1975, Franklin and Lieb 1979, Jeppesen 1987, Waldrip and Shaw 1979). The annual, MCP home-range area for wapiti in the Washington sagebrush-steppe, 162 km^2, was also smaller than that for MA wapiti (McCorquodale et al. 1989).

The MCP estimate for summer home-range sizes for wapiti in the sagebrush-steppe of Washington, 95 km^2 (McCorquodale et al. 1989), was smaller than that for wapiti in the INEL area, 165 km^2 and 245 km^2 for MA and CL wapiti, respectively (Table 3). Summer home-range sizes for wapiti and red deer in non-arid environments were also smaller, 1-31 km^2, than that for wapiti in sagebrush-steppe (Boer 1989; Catt and Staines 1987; Craighead et al. 1973; Edge et al. 1985; Edge et al. 1986; Franklin et al. 1975; Franklin and Lieb 1979; Georgii 1980a,b; Irwin and Peek 1983; Jenkins and Starkey 1982; Jeppesen 1987; Martinka 1969; Waldrip and Shaw 1979; Wallace 1991).

Mean daily distances travelled by wapiti during the summer in the INEL area were high in comparison with other investigations (Table 4). Wapiti in the Washington sagebrush-steppe travelled 2.2 km/day from June through August (McCorquodale et al. 1989), while Jackson Hole wapiti travelled 3.2 km from 16 July to 15 September (Martinka 1969). Wapiti in Arizona's White Mountains also travelled less during the summer, 7.5 km/day (Wallace 1991), than wapiti in the INEL area.

Thus, wapiti in the INEL area had the largest home-range sizes and longest daily distances of all investigations examined. Of course, it is important to keep in mind that these comparisons are more qualitative than quantitative in nature because of methodological differences. Confounding influences in home-range comparisons include home-range calculation method, number of relocations per home range, time period, and gender composition.

TABLE 3. Summary of summer, MCP home range areas for adult wapiti and red deer from 14 investigations. Reported measures of variation are not listed because they could not be standardized across the investigations.

Area (km^2)	Period	Elk[a]	Habitat	Source
1[b]	Jun-Sep	fr	spruce-fir-beech	Georgii 1980
2	1 Jul-15 Sep[c]	fr	spruce	Catt and Staines 1987
3[d]	Jun-Aug[c]	h	beech-redwood	Franklin et al. 1975
3	Mar-Sep[c]	fr	conifer-moorland	Jeppesen 1987
4	Apr-Nov	mr	spruce-fir-beech	Georgii 1980
4	1 Jul-15 Sep[c]	mr	spruce	Catt and Staines 1987
6	Apr-Aug	f	prairie-oak	Waldrip and Shaw 1979
8	16 Jun-8 Sep	f	cedar-hemlock	Irwin and Peek 1983
10	21 Jun-23 Sep	f	lodgepole pine	Craighead et al. 1973
11[e]	5 Jun-15 Sep[c]	f	spruce-hemlock	Jenkins and Starkey 1982
12	Jun-Sep	f	spruce-fir-alpine	Bear 1989
12	6 May-15 Sep	m	conifer	Martinka 1969
12	6 May-15 Sep	f	conifer	Martinka 1969
16	Jun-Sep	m	spruce-fir-alpine	Bear 1989
20	Jun-Aug	f	conifer-chaparral	Wallace 1991
31	Jun-Aug	f	conifer-chaparral	Wallace 1991
95	Jun-Aug	f	shrub-steppe	McCorquodale et al. 1989
118	Jun-Aug	m	shrub-steppe	McCorquodale et al. 1989
165	Jul-Sep	h	sagebrush	This study
245	Jul-Sep	h	juniper-lava	This study

[a]fr = female red deer, mr = male red deer, h = wapiti herd, f = female wapiti, m = male wapiti.

[b]Quadrat procedure.

[c]Home range size calculations involved periods other than summer.

[d]Boundaries based on vegetation types.

[e]95% probability ellipse.

TABLE 4. Comparisons of daily distances travelled by adult wapiti and red deer from 8 investigations.

Daily Distance (km)	Variation[a]	Method[b]	Sampling Period	Elk[c]	Habitat	Source
0.2	—[d]	mp	May	f	lodgepole pine	Craighead et al. 1973
1.2	—[d]	mp	June	f	lodgepole pine	Craighead et al. 1973
1.4	0.1	cr	annual	f	conifer	Edge and Marcum 1985
2.2	0.2	cr	summer	h	shrub steppe	McCorquodale et al. 1989
2.4	—	mp	fall	h	beach-redwood	Bowyer 1981
2.5	—[d]	mp	Aug	f	lodgepole pine	Craighead et al. 1973
3.0	0.4	cr	fall	h	shrub-steppe	McCorquodale et al. 1989
3.2	1.0-5.6	cr	16 July-15 Sep	f	conifer	Martinka 1969
3.2	0.2	mp	winter	h	conifer-chaparral	Wallace 1991
3.3	1.1-9.4	cr	6 May-15 July	f	conifer	Martinka 1969
3.5	0.6	cr	spring	h	shrub steppe	McCorquodale et al. 1989
4.0	0.5	mp	annual	fr	conifer-moorland	Jeppesen 1987
4.0	0.3	mp	spring	h	conifer-chaparral	Wallace 1991
4.2	—[d]	mp	Oct	f	lodgepole pine	Craighead et al. 1973
6.5	0.5	mp	fall	h	conifer-chaparral	Wallace 1991
7.5	0.3	mp	summer	h	conifer-chaparral	Wallace 1991
7.1	1.3	m2	June-Aug	f	juniper-lava	This study
12.6	3.6	m2	June-Aug	m	juniper-lava	This study
8.9	1.2	m2	June-Aug	f	sagebrush	This study
9.5	0.8	m2	June-Aug	m	sagebrush	This study

[a]Variations were either standard errors or ranges; — = unavailable.

[b]Distances were calculated from the following: cr = consecutive relocations, mp = multiple points over 24 hours, and m2 = day-night relocations <24 hours apart.

[c]fr = female red deer, h = wapiti herd, f = female wapiti, m = male wapiti.

[d]Data were from one animal.

Likewise, the quality of daily-distance estimates are affected by the gender composition and length of time periods between the relocations used.

Why do wapiti in the INEL area travel so much? Aridity may be a factor. Annual precipitation and annual, MCP home-range areas have been previously suggested to be related (McCorquodale et al. 1989). We agree with McCorquodale et al.'s (1989) point that while annual home-range area is highly correlated with annual precipitation, this relationship is not linear. That is, home-range size is influenced by multiple factors including forage availability, juxtaposition of resources, physiological state, cover quality, ambient temperature, habitat requirements, abundance of insects, difficulty of travel, population density, plant phenology, human disturbance, and social relationships (Craighead et al. 1973; Georgii 1980a,b; Jenkins and Starkey 1982; Irwin and Peek 1983; Edge et al. 1985; McCorquodale et al. 1989). For example, while it is true that the INEL area is more arid than the Washington sagebrush-steppe, human disturbance may be more of a constraint at the Washington site. We found wapiti home ranges did not conform to the INEL's boundaries; however, McCorquodale et al. (1989) found wapiti home ranges roughly matched the size and shape of an area free from human disturbance.

The key to explaining the large summertime movements of wapiti in the INEL area lies in understanding the motivation for the circadian pattern between the cropland and sagebrush habitats. Obviously, surface water was important. However, it was not the sole motivator, because in certain areas the wapiti were equally close to cropland and guzzlers that were in native vegetation.

Perhaps the key motivator is nutrition. This is unlikely, since the nutritional quality of the native forage was sufficient to meet elk maintenance requirements (J. C. Mosley, Univ. Id., unpubl. data). A worthwhile study would be to better separate the forage versus water needs of the INEL wapiti by manipulating crop types and irrigation regimes.

Juxtaposition of resources also provided an incomplete explanation (of at least differences

between the CL and MA herds) because inspection of topographic maps indicated distances between vegetation types used during the day and nearest cropland were similar; however, human-related disturbances differed between the wapiti herds. These disturbances appeared to affect at least the timing of cropland use. When MA wapiti were hunted during the summer, they limited the time they spent in cropland to early morning hours (roughly 0200-0400). This contrasts with the CL wapiti which were not subjected to depredation hunts and would enter cropland during daylight hours.

Jeppesen (1987) found similar circadian patterns among red deer in Denmark in a mosaic of conifer plantations, moorland, and grassland. Red deer bedded diurnally in forest cover and fed nocturnally in more open vegetation types. Jeppesen (1987) attributed this pattern as an adaptation to human disturbance which included hunting. This is also an appropriate hypothesis for wapiti in the INEL area because human access to INEL land was restricted creating a disturbance-free zone. Unfortunately, we were unable to quantify the human disturbance adjacent to INEL land. Still, human disturbance is also not the sole motivator because there were times when the CL wapiti were not being disturbed while on cropland, yet they maintained a circadian pattern.

A heat-stress hypothesis may be the best explanation. Heat stress increases maintenance requirements (Young 1988:461) and may cause ruminants to seek cover during the day and shift their grazing behavior to nighttime. Wapiti in the Washington sagebrush-steppe were noted to water at night and daily distances calculated with multiple relocations within a 24-hour period were comparable to those in the INEL area (McCorquodale, Pacific Northwest Lab., pers. commun.).

In conclusion, the most important (interrelated) factors causing the relatively large home-range areas found in our study are aridity, juxtaposition of habitat components, and human disturbance. Moreover, a heat-stress hypothesis best explains the circadian pattern of daily movements observed during the summer. This implies wapiti in any hot and arid environment would exhibit a similar pattern.

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Cannibalism by Black Bears in the Nimpkish Valley, British Columbia

Abstract

We studied black bears (*Ursus americanus*) between 1992 and 1995 in the Nimpkish Valley, Vancouver Island, British Columbia. During 1994, we observed 4 incidents of cannibalism by black bears. One incident of cannibalism occurred on a denned, radio-collared female that was consumed 390 m from her den and her two-cub litter that was consumed at the den site. The second incident involved a radio-collared male who consumed a female and her cub near their possible den site soon after den emergence. The third incident was one cub of a two-cub litter that was consumed 39 days after its radio-collared mother emerged from her den. The fourth incident was a subadult female attacked by an adult male during autumn before hibernation. Several authors have hypothesized that males kill unrelated cubs to increase their reproductive fitness. In our study, cannibalistic behavior of male bears is unlikely to have enhanced reproductive fitness because the bears involved were residents within their mating ranges, thus there is a high likelihood that the cubs were related to the aggressor. The high incidence of cannibalism in our study during 1994 is puzzling and inconsistent with explanations which attribute this behavior to enhancement of the fitness of male bears.

Introduction

Assessment of mortality is helpful in the management of wildlife populations. Of all the causes of mortality, cannibalism, although infrequent, is particularly interesting and least understood from an evolutionary perspective. There have been few documented cases of cannibalistic attacks by male black bears (*Ursus americanus*) on female black bears despite many studies in which bears have been monitored intensively (see Garshelis 1994). Garshelis (1994) found 39 known cases of intraspecific killings (excluding cubs) reported in 17 North American black bear studies that were conducted between 1975-92. Ten of the victims were adult females with cubs (four in dens) and 11 were subadult females. Although uncommon, cannibalism may be an important source of mortality in populations of black bears.

Several factors may affect the frequency of cannibalism within a population. Cannibalism appears to be density dependent in some vertebrate populations (e.g. Elwood 1992). However, in his review of black bear population processes, Garshelis (1994) did not find an association between high population densities and high rates of cannibalism. The sex-age composition of the population may also affect the rate of cannibalism. Much of this cannibalism is inflicted on cubs. In Arkansas, a male dominated sex ratio may have led to an increased rate of cannibalism among black bears (Clark 1991). In one population which was comprised of 59% adult and subadult males, cub survival rate was 0.31. In another population which was comprised of 39% males, cub survival rate was 0.90. Causes of cub mortality were unknown, but Clark (1991) suspected that the male-dominated adult sex ratio was a factor in low cub survival.

Although cannibalism by black bears is uncommon, we observed four incidents during 1994 on northern Vancouver Island. This frequency of cannibalism is much greater than that reported from other studies. Our objectives are to describe the incidents and discuss possible causative factors.

Study Area and Methods

The incidents of cannibalism that we report occurred in 1994 while monitoring 19 radio-collared black bears (7 females, 12 males) as part of the 3-year Nimpkish Black Bear Study. The study area was located in the Nimpkish Valley, 40 km south of Port McNeill on Vancouver Island, British Columbia. The forests in the area have been commercially harvested by clearcutting since the 1920's. Most of the cutovers have regenerated to conifer-dominated, second growth stands with closed canopies. Because of recent logging, a few early seral stage cutovers occur in a mosaic of second growth and some old growth stands. Bears were captured in culvert traps or by Aldrich foot snares, immobilized using Telazol (Ayerst Laboratories, Montreal), and radio-collared. Radio-telemetry was conducted by ground and

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air at least twice weekly from the spring of 1992 to 1995. Home ranges were determined from a minimum of 95 locations for the bears involved in the cannibalism incidents.

Results

Trapping success, based on 49 captures of 34 individuals (25 males and 9 females), indicated that there were more males than females in the black bear population (2.8 males : 1 female; $\chi^2 = 7.53$, d.f. = 1, $P < 0.006$). This ratio is biased because males were easier to trap than females; the recapture rate of males was 36% while that of females was only 10% (Table 1). Despite this trapping bias, visual sightings of uncollared bears corroborated our trapping results and confirmed that the population had a male-dominated sex ratio. Our preliminary estimate of population density in the area that the cannibalism occurred (0.25 bears/km^2) reveals that the density of black bears is not abnormally high compared to elsewhere in North America (range 0.07-1.30 bears/km^2, Garshelis 1994).

The first case of apparent cannibalism of a female and cubs was encountered on 26 April 1994. An 11-year-old radio-collared female (F03) with cubs (one of four collared reproductive adult females) apparently left her den site between 20-22 April. On 26 April, we approached the den site to determine the type of den structure that she used. When we reached the den, an uncollared bear was nearby and ran away. A bear bed was 5 m from the den, and bear hair and cub claws (21 in total) were found in bear scats located at the bed and around the den. The den bedding was intact and there were no signs of struggle at the den site. The den was in a spaced second growth stand beneath a root bole and had three entrances. At the time of the first investigation, we believed that F03 was alive and 390 m from the den. Three days later she was found dead at the same location, with a radio-collared male (M08) and an unmarked bear feeding on her body. An investigation of F03's body later revealed a large hematoma in the hide, suggesting that she was injured before death, perhaps while defending her cubs.

The second case of cannibalism on a female and cubs became evident after a 6-year-old radio-collared male (M06) had not moved from a closed canopy second growth stand for eight days, beginning 19 April 1994. The body of a partially consumed adult female was discovered when we approached and scared M06 away. The site was very disturbed, including marked trees, marked trails, and masses of ferns used to cover the body. There were a few beds and numerous scats, some of which contained bear hair and cub claws (eight claws were found). The female's face was not damaged and there were no signs of fighting.

Later during summer, we searched the area surrounding the site where the female's carcass was found. A den was found under a root bole in a small patch of old growth, 180 m from the body site. The den was used the previous winter but we cannot definitively state that this den was used by the female and her cub. A well-lined bed was found 17 m from the den, suggesting that the female was not in the den when the attack occurred (if the den was hers). A large heavily-climbed tree was between the den site and the body site, next to which we found signs of a food cache and marking of small trees. A tooth and thin skull fragments from a young cub were retrieved from this cache. Our evidence suggests that the attack started at, or near, this climbed tree.

A third case of cannibalism was observed 12 June 1994. Thirty-nine days after emerging from her den, a radio-collared female (F01) was located in a cutover that she used regularly. She was bawling and vocalizing to one of her two cubs-of-the-year which had climbed a small conifer tree at the cutover's edge. The second cub was not seen. A large 11-year-old radio-collared

TABLE 1. Recapture rates of individually marked black bears in the Nimpkish Valley, Vancouver Island, 1992-1994.

	Number of individuals captured	Number recaptured	Total number of bears captured	Percent recaptured
Female	9	1	10	10
Male	25	14	39	36
Total	34	15	49	31

male (M15) was at the site, but was not visible to us. We returned to the site 6.5 h later and observed the cub still in the tree. Subsequent investigation confirmed that M15 had consumed one of the cubs and bedded at the base of the tree which the surviving cub had climbed. Scats next to the beds contained cub claws. Large claw marks in the bark of the tree suggested that M15 had attempted to climb up after the surviving cub. This cub was seen alive the next day but not afterwards, although the mother was observed repeatedly over the summer. She did not produce cubs in 1995.

Eight days later in the same cutover, M15 treed another radio-collared 5-year-old female (F06) and her two cubs-of-the-year. Both cubs were seen the next day. Although F06 was monitored regularly, she was not seen again for 58 days and was accompanied by only one cub at this next sighting. Besides these attacks on females and their cubs, M15 was observed the previous spring in a brawl with another radio-collared adult male close to the cutover in which he treed the females and their cubs.

The fourth case of cannibalism occurred on 6 November 1994. During regular monitoring of radio-collared bears, a 6-year-old male (M11) and a 4-year-old female (F07) were located close together. Loud vocalizations were heard upon walking closer to the pair. Bawling, huffing, and strange vocalizations appear to have been made by the female. The two bears were only 15 m from the observers in an 18-year-old second growth conifer stand but were very difficult to observe amongst the thick vegetation. An aggressive interaction between the two bears was not suspected because they and two other females used the same cutover almost year round. Furthermore, the two bears were seen together during the 1994 breeding season.

We thought that the bears may be consuming a deer carcass and decided to interrupt the interaction and investigate the site. We attempted to chase away both bears. M11 eventually left very slowly but remained close to the site. F07 refused to leave the site but stopped her vocalizations when we made a lot of noise. We were able to walk to within 5 m of F07. Her hind legs appeared to be partly immobilized when she attempted to drag herself away. The injuries appeared to be serious and we believe she would have been killed had we not intervened. We suspect that M11 had been involved in cannibalism before, because he had eaten a young male bear during the spring. Evidence of cannibalism was more circumstantial in that situation because the young male's body was close to human activity and may have been killed by humans.

We decided to intervene for three reasons: 1) F07 was an important study animal because she was one of two subadult females that had been followed for 1.5 years; 2) because of the previous three cases of suspected cannibalism in the spring, we wanted to determine the cause of her injuries; and 3) hunters were in the area and we wanted to determine if her initial wounds were due to gunshot. If M11 was allowed to consume the female we would not know the cause of her injuries.

F07 was immobilized and examined. Her injuries were extensive. Her right thigh had a large deep wound, 15 cm long x 10 cm wide, which extended down to the femur. A second large wound was located below and to the left of her anus. It was about 10 cm long but not as open as the thigh wound. The wounds were not caused by gunshot. It appeared that F07 had lost a lot of blood because her gums and tongue were whitish and cold. F07 was moved away from M11 to another location within her home range. Although F07 recovered from the drugs and was observed standing on her front legs, she never left this new site and died two days later from infection of her wounds. M11 remained close to the attack site for another day and then moved away. We do not believe he was nutritionally stressed because he was very fat and had consumed a deer 19 days before. A later investigation of the site revealed a large amount of bear hair with skin attached spread around a few flattened areas and on numerous shrubs. No meat or other attractants were found at the site. F07 had not yet denned, although other females had started to enter their dens. We later examined her decomposed body and found that none of her bones were broken.

In addition to these four cases of cannibalism during 1994, we observed two incidents in 1992 of male bears treeing females and their cubs at the edges of cutovers during early spring. The bears were not radio-collared and so the outcomes are unknown. It is possible that M15 was involved in the 1992 incidents because although he was unmarked at the time, these areas were part of his home range in 1994. To our knowledge no

cubs were born in the study area during 1993. Besides the scats at the cannibalism sites described above, three bear scats containing cub claws were found incidentally in the study area between 1992-94.

Discussion

During 1994, there appeared to be a high rate of cannibalism among black bears in the Nimpkish Valley study area. Within one year, we documented four attacks: three involving cubs (two of which included the death of the mothers) and one attack on a subadult female. Other researchers (Rogers 1983, Alt and Gruttadauria 1984, Tietje et al. 1986) have reported these types of killings, but none report as many incidents within such a short time.

The role of cannibalism in population processes is not well understood. Incidents of cannibalism in northeastern Alberta described by Tietje et al. (1986) involved unrelated individuals and a female from outside the mating range of the predatory male. Tietje et al. (1986) hypothesized that killing cubs by male black bears was adaptive under particular conditions: males out of their mating range encountering bears that are not their kin. Males are thought to kill unrelated cubs to increase their reproductive fitness.

The rationale for cannibalism presented by Tietje et al. (1986) may not pertain to our study. In our study area, at least two of the incidents in which cubs were killed involved resident males in their mating ranges and resident females. The cannibalistic behavior of male bears which we observed is unlikely to have enhanced their reproductive fitness because the bears involved were within their mating ranges, thus there is high likelihood that the cubs were related to the aggressor. Furthermore, the killing of adult and subadult females by males seems particularly maladaptive because it would diminish the male's reproductive opportunities in the future.

Several factors may contribute to the high rates of cannibalism that we observed. Skewed sex ratios may affect the rate of cannibalism within bear populations (Garshelis 1994, Wielgus and Bunnell 1994). The bear population in our study area likely had more males than females. In populations that are dominated by males, females would encounter many males over the breeding season. The following year when males encounter cubs there would be a lower likelihood that the cubs are theirs. Hunting of adult male bears by humans in such areas could further exacerbate cannibalistic attacks by causing influxes of subadult male bears (Wielgus and Bunnell 1994).

In addition to a sex ratio dominated by males, habitat alteration may increase aggressive interactions among bears. Much of our study area is managed for conifer production and thus dominated by closed canopy second growth forests. The few early seral stage cutovers which provide foraging habitat during spring result in seasonal concentrations of bears. These local high densities of bears may increase interactions between adult male bears and females with their cubs. Availability of den sites may also be affected by habitat alteration. Bears in the Nimpkish Valley den in large hollow trees, root boles and logs that may not persist after logging (unpub. data). Removing the structures used for denning may increase the vulnerability of females with cubs by limiting the supply of secure den sites. Females with cubs are in dens after males have emerged thus are vulnerable to attack (Tietje and Ruff 1980). If females are forced to use less secure dens (e.g. more than one small entrance) they increase their already vulnerable situation.

Some of the killings of adult females that we observed in the Nimpkish Valley study may have been a consequence of the attempts by the mothers to protect their cubs. The rationales argued to explain cannibalism in previous publications could apply to some of our observations but other incidents appear inconsistent with tactics to increase reproductive fitness of male bears.

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Biology and Habitat Use of the Mazama Pocket Gopher (*Thomomys mazama*) in the Puget Sound Area, Washington

Abstract

The ecology and distribution of the Mazama pocket gopher is poorly understood and several subspecies are being considered for state and federal protection. We studied Mazama pocket gophers near Olympia, Washington from February-April 1992 and in April 1995 to describe their biology and habitat use as part of a larger assessment of experimental population control methods. Males were significantly larger than females in mass and standard body measurements. Gophers from two sites, Lacey and Olympia, Washington, had similar physical measurements, although gophers near Lacey weighed more and had longer tail and hind foot lengths, while gophers near Olympia had longer ear lengths. Olympia males had longer baculum lengths. The capture of pregnant and lactating females and dual occupancy of some burrows by males and females indicated that breeding activities were underway during this period. There was a nearly 1:1 sex ratio of males to females. Densities were lower (10/ha) near Lacey in an orchard with mowed grass and forb understory and past population control than for an unexploited population at the Olympia site (60/ha), containing a Christmas tree plantation with an understory of orchard grass and the invasive, introduced Scotch broom. Food caches occurred about 53 cm in depth and held about 200-250 g of root cuttings (2,500 g maximum), indicating that gophers in the area fed heavily on thistle and Scotch broom. Pocket gophers reinvaded 22 of 25 (88%) burrow systems within 10 weeks after removal trapping. The conflicting goals of population control to reduce agricultural damage versus protection of rare or threatened pocket gopher subspecies requires better information on taxonomy, distribution, and population status of subspecies. Limited home range sizes (108 m^2 for males; 97 m^2 for females), dependence upon common herbaceous and woody foods, and rapid reinvasion rates suggest that rare subspecies may be readily managed if taxonomic and population issues are clarified.

Introduction

Three genera of pocket gophers (*Geomys, Pappogeomys, Thomomys*) occur in North America (Hall 1981). These fossorial mammals are uniquely adapted to a life of extensive underground burrowing with the exploitation of a wide array of above and below ground vegetation for food (Chase et al. 1982, Nevo 1979). They may play important ecological roles in soil aeration, mixing, and drainage, and in the distribution and succession of plant species and communities (Chase et al. 1982). Additionally, gophers are preyed upon by numerous avian and mammalian predators, and their burrows (active and abandoned) are used by other animal species (Chase et al. 1982). Ecological equivalents to pocket gophers occur on most continents (Nevo 1979).

The taxonomic classification of pocket gophers in North America is in a state of flux and more than 300 species and subspecies have been described (Hall 1981). This may relate to the fact that populations of pocket gophers have significant genetic plasticity and are easily isolated by any of several factors: rocky, poorly drained, or excessively compacted soils; extensive forest cover with little understory vegetation; or land use practices such as extensive and regular plowing (Hall 1981). Little is known about the fossorial western pocket gopher (*Thomomys mazama*) of western Washington and Oregon despite their economic importance and uncertain population and taxonomic status (Witmer 1992). The original work of Dalquest and Scheffer (1944) still serves as the basic source of information on the species. Several of the six subspecies occurring in the Puget Sound area are being considered for federal or state protection (Washington Department of Fish and Wildlife 1994). At the same time, pocket gophers are generally considered a major pest in many agriculture and reforestation areas and are the object of extensive control efforts (Case 1983, Chase et al. 1982, Teipner et al. 1983). Consequently, it is important to learn more about the

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biology, habitat use, distribution, and taxonomy of this species so that appropriate management decisions can be made. We collected data on the biology and habitat use of Mazama pocket gophers during field trials of experimental methods of population control in the Lacey, Washington (1992) and Olympia, Washington (1995) areas.

Study Area and Methods

Field data were collected at the Washington Department of Natural Resources' Meridian Seed Orchard, near Lacey (1992) and at the Olympia airport (1995), Thurston County, Washington. The sites are about 15 km apart. The Orchard is located in T17N, R1W, Section 1. The airport is located at T17N, R2W, Section 14. The sites are in the Puget Sound Area of the Western Hemlock (*Tsuga heterophylla*) vegetation zone (Franklin and Dyrness 1973). The most common tree species in the area is Douglas-fir (*Pseudotsuga menziesii*). The areas are at about 50 m above mean sea level and receive about 90 cm of precipitation annually. Soils are Tumwater gravelly-sandy loams and derive from glacial drift and outwash. The Lacey study was conducted on an 3.3 ha mowed field that had been forested until about 1985. Tree stumps were removed and the area was converted to agricultural use. After an oat crop was produced on the site for two seasons, the field has been fallow and mowed once per year. The Olympia study was conducted on 0.6 ha of Christmas tree plantation with an understory dominated by orchard grass (*Dactylis glomerata*) and Scotch broom (*Cytisus scoparius*). Because of the mild climate, well-drained soils, abundant herbaceous vegetation, and lack of tree cover canopy cover, both sites can be considered to represent good quality pocket gopher habitat and are probably typical of many non-forested areas in the Puget Sound area.

During late February 1992, pocket gophers were live-trapped, anesthetized with methoxyflurane, and 6 g radiocollars and leg bands attached. Animals were allowed to recover and then released back into their burrow opening. Twenty-five animals were radiocollared at the Lacey site. Each animal was located daily and monitored briefly for movement/activity. The final radiotelemetry data were collected in early April 1992. Consequently, data presented here on densities, home ranges, and burrow, nest, and food cache depths represent the late winter/early spring period. This is a period when only adults and subadults (not juveniles) are present. Animals recovered dead during the course of an experimental toxic bait study were recovered and necropsied. In addition to mass at the time of capture, information was obtained from necropsies on standard body measurements, sex, and reproductive status. Animals still alive at the end of experimental field trials or with nonfunctional radiotransmitters were recovered by live-trapping, euthanized, and necropsied. During a four day period in April 1995, pocket gophers were live-trapped or kill-trapped at plots at the Olympia site. Information on mass, standard body measurements, sex ratio, and density were recorded. T-test analyses were performed to test for differences between sexes and between study sites and evaluated at the a=0.05 significance level.

Results and Discussion

Twenty-five pocket gophers were captured, radiocollared, and monitored over the course of about 40 days of field trials at the Lacey site. Because of the timing of these field trials, all animals were 1+ years old (i.e., adults and subadults); some were probably about to enter their first breeding cycle. Information on mass and standard body measurements are presented for nine females and ten males (Table 1). Data on six animals were not obtained because the animals had radiocollars chewed off and were never recovered (N=2) or succumbed to predation (N=4). Data are also presented for 21 females and 17 males from the Olympia site (Table 1). Males were significantly heavier and larger than females, but there was overlap in the range of masses and measurements (Table 1).

Despite the fact that the two sites are only about 15 km apart, we found significant differences in some masses and body measurements between the two populations of females and of males. The Lacey gophers had been captured about a month earlier in the year than the Olympia gophers, but this does not entirely account for the heavier body masses from the Lacey site. Five of the Lacey gophers captured and weighed in late February were also captured and weighed in early April (the latter being the time period of capture of the Olympia gophers). These Lacey gophers had declined somewhat in weight, but not significantly (t-test = 1.2, 8 df, p = 0.267). Lacey females were

TABLE 1. Average weights and standard body measurements (SD) for male and female pocket gophers, *Thomomys mazama,* collected near Lacey and Olympia, WA, during 1992, and 1995, respectively.[a]

Sex & Study Site	Weight (g)	Total Length (mm)	Tail Length (mm)	Hind Foot Length (mm)	Ear Length (mm)	Baculum Length (mm)	Max. Testis Length (mm)
A. Females:							
Lacey (N=9)	126.7* (14.1)	211.1 (7.8)	60.1* (5.0)	28.0 (1.6)	7.0* (0.0)	—	—
Olympia (N=21)	104.1* (14.9)	205.2 (6.2)	54.2* (4.8)	27.0 (1.0)	7.5* (0.6)	—	—
	p=0.001	p=0.066	p=0.010	p=0.108	p=0.022		
B. Males:							
Lacey (N=10)	146.7 (16.9)	221.8 (8.4)	62.2* (4.3)	30.2* (2.1)	7.7* (2.2)	24.3* (2.2)	12.4 (1.5)
Olympia (N=17)	134.6 (10.4)	223.2 (7.0)	57.2* (4.7)	28.5* (0.7)	8.4* (0.5)	26.6* (1.9)	13.4 (0.8)
	p=0.061	p=0.667	p=0.011	p=0.033	p=0.017	p=0.015	p=0.072
C. Sites Combined:							
All Females (N=30)	111.0* (17.9)	207.0* (7.1)	56.1* (5.5)	27.3* (1.3)	7.4* (0.6)	—	—
All Males (N=27)	139.1* (14.2)	222.7* (7.4)	59.1* (5.1)	29.1* (1.6)	8.1* (0.6)	25.7 (2.3)	13.0 (1.2)
	p=0.000	p=0.000	p=0.036	p=0.000	p=0.000		
D. Sexes Combined:							
Lacey (N=19)	137.2* (18.4)	216.7 (9.6)	61.2* (4.6)	29.2* (2.2)	7.4* (0.6)	—	—
Olympia (N=38)	117.8* (20.1)	213.3 (11.1)	55.6* (4.9)	27.7* (1.1)	7.9* (0.7)	—	—
	p=0.000	p=0.250	p=0.000	p=0.010	p=0.008		

[a]Paired values in columns marked with asterisks are significantly different (P<0.05).

significantly heavier, somewhat longer in total length, and had significantly longer tails and shorter ears (Table 1). They had similar hind foot lengths. Lacey males were somewhat heavier, had similar total lengths, had significantly longer tails and hind feet, but significantly shorter ears (Table 1). Baculum lengths were significantly longer in Olympia males, but testes lengths were similar. This pattern was also observed when the sexes at each site were combined: Lacey gophers were significantly heavier, somewhat longer, had significantly longer tails and hind feet, but significantly shorter ears (Table 1). This result is interesting because the two sites are presumably within the range of the same subspecies, T. m. tumuli. Smith and Patton (1980) noted that genetic variation and a lack of breeding barriers between isolated gopher populations can occur because of occasional influx of dispersing individuals, whereas gopher morphology may vary substantially between nearby populations because of a more direct response to environmental conditions (e.g., soil type, weather regime, available forage). Hence, they suggest less taxonomic splitting of isolated gopher populations into distinct species and subspecies. The masses and measurements we report are in about the middle of the range published by Ingles (1965) and Hall (1981) for T. mazama. We note, however, the difficulty of identifying subspecies based on external measurements and weight of specimens in the hand: most of the six subspecies' measurements and weights given by Dalquest and Scheffer (1944) fall within ±1 standard deviation (SD) unit of our masses and measurements and all fall within ±2 SD. Considerably more research may be required to resolve taxonomic issues of isolated gopher populations in the Puget Sound area.

The sex ratio of males and females at the Lacey site was not different from a ratio of 1:1 (9 females, 10 males). Five of 23 field estimations of sex of live animals, based on palpation of baculum and pubic gap, proved to be in error (22%) when estimates were later compared with necropsy results. We caution researchers not to rely too heavily on results of sexing live animals in the field. McCravy and Rose (1992) provided similar warnings to researchers regarding the determination of reproductive status of live, in-hand, small mammals. The sex ratio of gophers at the Olympia site was somewhat skewed towards females (21 females, 17 males), but suggests a nearly 1:1 ratio.

Baculum length averaged 25.7 mm (SD = 2.3; range = 20-30; n = 27) and fell within the range reported by Ingles (1965) and Hall (1981) for T. mazama. The measurement is useful to distinguish *T. mazama* from all other species of Thomomys, but is not generally used to distinguish subspecies of *T. mazama*. Despite overlap in the ranges of baculum lengths, we found a significant difference in lengths between the two sites, suggesting that this measurement may be useful in distinguishing populations of *T. mazama* in the Puget Sound area. Testes, with the exception of one individual, were both developed with one usually 1-2 mm larger (in the long axis) than the other. The average maximum length of the larger testis was 13.0 mm (SD = 1.2; range = 10-15; n = 27) and was similar between sites.

One of the 9 necropsied females at the Lacey site was pregnant, bearing 7 fetuses (2 large, 5 small). Three other females were post-partum with turgid uteri and swollen teats. Five placental scars were observed in one of these uteri, 2 in another; none could be discerned in the third. Litter sizes reported in the literature average about 5, but range from 2-8 (Chase et al. 1982, Ingles 1965). Five of the 9 (56%) females necropsied from the Lacey site were not pregnant or post-partum, but the study was conducted relatively early in the breeding season. A higher incidence of pregnant or post-partum individuals may have been observed 1 or 2 months later (Verts and Carraway 1991). At the Olympia site, 19 of 21 females (90.5%) were not pregnant at the time of capture. Two females (9.5%) were pregnant, each carrying 4 fetuses.

The gopher population at the Lacey site occupied a field that had been densely forested about 6 years before the study. Prior to tree harvest, the forested area probably supported few gophers because gophers require the forbs and grasses of an early successional stage for food. Additionally, gopher population reduction activities after forest removal occurred on several occasions in recent years. Information on Mazama pocket gopher distribution in the Puget Sound area is primarily based on Dalquest and Scheffer (1944). At that time, disjunct populations occupied nonforested areas, primarily glacial-outwash prairies. Very few locational records of western pocket gophers are in the Priority Habitats and Species database (Washington Department of Fish and Wildlife, unpubl. data, 1995). We speculate that the current distribution of pocket gophers may differ with populations being more widespread because of extensive deforestation in the south Puget Sound area. For example, aerial photographs of Thurston County, WA, which was historically largely forested, show large areas that have been deforested for urban development, agriculture, right-of-ways, and other development (Pringle 1990). Updated distribution maps are needed before informed management decisions can be made on the need for protection and the threat of new developments on specific subspecies.

The population at the Lacey site occupied a 3.3 ha field which contained at least 32 individual burrow systems; a few systems with little surface activity may have been overlooked. Consequently, we estimate a minimum subadult/adult density of 10 gophers per ha. Later in the year, after production of young, the density could become much greater (perhaps 5 times larger) until dispersal occurred. During March, while live-trapping animals to recover radiocollars, we caught 2 adults in each of several burrow systems, indicating the mating season was underway, as has been noted by others (Marsh and Steele 1992; Teipner et al. 1983). Gopher densities at the Olympia site were 6 times higher (60 per ha), perhaps because of more favorable habitat or because gopher populations there had not been previously reduced by the use of toxicants or kill traps as on several occasions in recent years at the Lacey site. At least five of these burrow systems were occupied by an adult male and female.

Home ranges for males (108 m2; SD = 37.9; range = 73-143; n = 4) were somewhat larger than for females (97 m2; SD = 57.1; range = 47-151; n = 4) at the Lacey site. These home ranges are somewhat smaller than figures reported in the literature for the species and subspecies of Thomomys (Chase et al. 1982; Teipner et al. 1983). Because we only monitored animals at this study site between February-April, 1992, it is possible that annual home ranges for pocket gophers would be somewhat larger. Marsh and Steele (1992) noted, however, that home ranges for pocket gophers are relatively uniform throughout the year. It is also possible that the field, with its dense herbaceous plant cover mowed only once per year in the late summer or fall, provided for the food requirements of individual pocket gophers in a relatively small area. Home ranges are generally smaller in better quality habitat (Chase et al. 1982; Marsh and Steele 1992). Some radiocollared pocket

gophers were recovered dead in their nests because part of the Lacey study was a test of an experimental rodenticide. These nests were at an average depth of 88.5 cm (SD = 25.9; range 48-150; n = 12). The chambers were roughly ovoid in shape, about 25 cm in diameter and 15 cm in height, and consisted of dry grass often with a few pieces of plastic and root cuttings. The nests were notably clean as excretory wastes were deposited in nearby fecal chambers.

We occasionally encountered food caches while excavating pocket gopher nests or burrows. Gophers typically clip and cache fleshy and succulent roots and stems (Marsh and Steele 1992). Five caches at the Lacey site averaged a depth of 52.8 cm (SD = 15.0; range = 36-72). These chambers were about 30-60 cm from the nest, were about 23 cm in diameter and about 18 cm in height. They were usually full of a single type of root cuttings with segments 2.5-5 mm in diameter and about 3 cm long. The most common plant species were thistle (*Cirsium* spp.) and Scotch broom (*Cytisus scoparius*). Most caches contained about 200-250 g of cuttings, but one cache had about 2,500 g of cuttings. One food cache at the Olympia site was encountered; it contained root cuttings of Scotch broom and weighed 782 g.

While many burrows were located in the top 25 cm of soil at the Lacey site where foraging in the high density root zone occurs, some were much deeper. Based on the recovery of 5 radiocollared gophers from burrows, deep burrows averaged 141 cm in depth (SD = 21.9; range = 119-150). Deep burrows may provide important refugia during inclement weather and may help drain the burrow system during periods of heavy or prolonged rainfall (Teipner et al. 1983).

During the course of the Lacey study, 4 of 25 (16%) radiocollared gophers were taken by predators. The most common predator was believed to be red-tailed hawks (*Buteo jamaicensis*). Because an experimental rodenticide was being used, however, we cannot be sure that this rate reflects a natural rate. Mortality rates may be very high in late summer/fall when juveniles are dispersing (Marsh and Steele 1992).

We rechecked the 25 burrow systems at the Lacey site 10 weeks after all 25 radiocollared adults and several presumptive mates had been removed. Twenty-two of 25 (88%) systems were reoccupied, based on the open hole occupancy method (Barnes et al. 1970). Consequently, there appears to be a high reinvasion rate of burrow systems as noted by others (Marsh and Steele 1992; Teipner et al. 1983). Because of the large investment of energy in making a burrow system, burrows are believed to be a valuable resource sought out by dispersing gophers (Reichman and Smith 1990).

It is apparent that more research is needed to determine the distribution and status of subspecies of western pocket gophers in the Puget Sound area. It is also apparent that pocket gopher populations can vary in numerous morphological characteristics despite relatively close (15 km) proximity. Better documentation of these differences may help managers and interested parties more readily identify endangered from non-endangered subspecies of pocket gophers. Management of rare or threatened pocket gopher subspecies should be possible by providing adequate burrowing and foraging habitat, if subspecies can be more readily identified and monitored in the future.

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Dietary Similarity in Sympatric Idaho and Columbian Ground Squirrels (*Spermophilus brunneus* and *S. columbianus*)

Abstract

We studied diets of *Spermophilus brunneus,* a rare endemic species, and *S. columbianus,* a larger, widespread potential competitor, in two areas where they were sympatric to learn if competition for food might be a factor in *S. brunneus'* rarity. Because the diet of *S. brunneus* was unknown, we also wished to determine if dietary specializations might explain the species' limited distribution. Vegetation at the study sites was sampled using a point frame method. Fecal pellets were collected from live-trapped squirrels and analyzed using a microhistological technique; plant parts (leaves/stems, seeds/flowers, roots/bulbs) were tallied as separate categories for each species. At the two sites, *S. brunneus* consumed 45-50 species of plants in 55-75 categories, although only 18-20 categories comprised >1% of the diet and only 5-7 comprised >5%. Similarly, *S. columbianus* consumed 53-58 plant species in 74-75 categories; only 10-17 categories comprised >1% of the diet and only 4-6 comprised >5%. Idaho and Columbian ground squirrel diets were 30-52% similar at a site, whereas each species' diet was only 25-37% similar between sites. Diets were not correlated with plant abundance in the habitat, indicating that diet selection was taking place. The diet of *S. brunneus* appears typical of ground squirrels of the subgenus *Spermophilus*. Both species utilized similar resources, and habitat segregation probably accounted for most of the observed dietary differences. The results suggest that dietary overlap with *S. columbianus* relegates *S. brunneus* to less productive habitats and is a factor in *S. brunneus*' rarity.

Introduction

The Idaho ground squirrel (*Spermophilus brunneus*) is one of the rarest North American mammals. It has the smallest geographic range of any *Spermophilus*, and certainly one of the smallest ranges among North American mainland mammals (maps in Hall 1981). Further, it is rare within its limited range (pers. obs.). This research was part of an effort to determine why *S. brunneus* is so rare.

Ground squirrels of the subgenus *Spermophilus* have similar diets and habits, and their geographic distributions are almost always allopatric or parapatric (Howell 1938, Durrant and Hansen 1954, Turner 1972, Hall 1981). However, throughout much of its 125 x 90 km geographic range in west-central Idaho (Yensen 1991), the endemic Idaho ground squirrel is sympatric with the widely-distributed Columbian ground squirrel (*S. columbianus*).

Columbian ground squirrels are about one and a half times as large as Idaho ground squirrels (head and body 245-300 mm vs. 160-190 mm) and two to three times as massive (450 vs. 170 g, lean weight of adult males; E. Yensen, unpublished data) and thus would have an advantage in an aggressive interaction. Optimal foraging studies of *S. columbianus* found that they attempt to maximize energy intake rather than maximizing nutrient intake or minimizing feeding time (Belovsky 1986, Ritchie 1988, Ritchie and Belovsky 1990). If *S. brunneus* followed a similar strategy, and if diets were similar, then in order for the two species to coexist sympatrically we would predict that the larger species would utilize the most productive habitats, and relegate the smaller species to habitats too unproductive for the larger competitor.

Consistent with this expectation, in Adams County, Idaho, Columbian ground squirrels occupy mesic meadows, forest edges, sparsely-timbered areas with open canopies, and fields, but do not occur in the more sparsely vegetated, rocky, xeric meadows with shallower soils associated with *S. brunneus*. Some meadows have both xeric and mesic vegetation as a result of a mixture of deeper and shallower soils, and in these the two species may occur adjacent to each other, with *S. columbianus* always in the more mesic habitat. Plant species composition differs strikingly in the mesic and xeric portions of the meadow, with xeric areas having obviously less total plant cover, fewer grasses, more forbs, and plants of shorter stature (E. Yensen, unpublished data).

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At meadows with both species, we have occasionally observed them foraging within a few meters of each other in ecotones, and we have also observed individuals of each moving up to 100 m from nest burrows to forage. Thus, both species potentially had access to the same resources, although in actuality there was habitat segregation with only a small area of overlap (<500 m2).

The only published information on Idaho ground squirrel diets is one anecdotal foraging observation (Davis 1939:184). Columbian ground squirrels eat mostly grasses, herbs, fruits, and bulbs (Howell 1938). In central Idaho, Lambeth and Hironaka (1982) found 43 species in their diet, of which silky lupine (*Lupinus sericeus*), yarrow (*Achillea millefolium*), grasses and sedges were the most important, whereas Elliott and Flinders (1985) found balsamroot (*Balsamorhiza saggittata*), yarrow (*Achillea millefolium*), clover (*Trifolium* spp.), fleabane (*Erigeron speciosus*), silky lupine (*Lupinus sericeus*), alpine timothy (*Phleum alpinum*) and bluebunch wheatgrass (*Agropyron spicatum*) were most important. In British Columbia, clover (*Trifolium dubium*), bentgrass (*Agrostis alba*), Kentucky bluegrass (*Poa pratensis*), and dandelion (*Taraxacum officinale*) comprised 98% of the diet (Harestad 1986).

The purpose of this investigation was to determine if indeed Idaho and Columbian ground squirrels had similar diets in areas where they co-occur as a step toward understanding the relations between the two species in areas of potential competition. A secondary goal was to determine if *S. brunneus* had any dietary specializations that might be responsible for its restricted distribution.

Study Sites

Two sites approximately 35 and 45 km NW of Council, Adams Co., Idaho where *S. brunneus* and *S. columbianus* foraged in close proximity were selected for study.

"Huckleberry." This site (Fig. 1) was in a 10-ha meadow surrounded by ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), and grand fir (*Abies grandis*) forest and was located 1.6 km N, 1.6 km E of Bear Guard Station, Adams Co., Idaho (45°05'N, 116°37'W, 1490 m elev.). The lower (southern) portion of the meadow was inhabited by Columbian ground squirrels, had soils >2 m deep, and was dominated by grasses and associated forbs. In the upper meadow there was a series of low, xeric, rocky ridges with shallow soils generally <1 m deep and intervening grassy swales that were inhabited by Idaho ground squirrels. There was a sharp contrast in vegetation cover between the xeric and mesic areas inhabited by the two species. Squirrel trapping and vegetation analysis were done in an area of ca. 2 ha that included both habitat types and the ecotone. The site was grazed by cattle in late summer. (See Yensen et al. [1991] for additional site description).

"Squirrel Valley." This site (Fig. 2) was at the SE edge of a 5 km^2 meadow between Bear and Steve's Creeks, 1 km S and 1 km E of Bear townsite (45°00'N, 116°39'W, 1320 m elev.). The study site spanned Steve's Creek. Columbian ground squirrels occupied most of the creek bottom and hillside to the east. The soils in the area occupied by *S. columbianus* were >2 m deep and the area supported a lush growth of mostly native and a few introduced grasses and forbs. Just east of the study site boundary was a hayfield with alfalfa (*Medicago sativa*). In the bottom west of the creek was an ecotone occupied by both species of ground squirrels. Further west was a steep bank about 8 m tall with well-drained, gravel soils. Above this was a grassy swale on shallower soils (<1 m deep to a clay layer) which supported a dense Idaho ground squirrel population. The vegetation analysis and squirrel trapping were done in an area of ca. 3 ha that included areas occupied by both squirrel species and an ecotone. The site was on a cattle ranch, and was moderately grazed at intervals throughout the growing season. Native vegetation had been partly replaced with introduced pasture grasses. There was much less contrast in vegetation structure or composition between the areas occupied by the two species of ground squirrels than at Huckleberry.

Methods

Ground squirrels were trapped using unbaited 14 x 14 x 41 cm Tomahawk traps or burrow entrance traps (Wobeser and Leighton 1979) set at burrow openings immediately after a squirrel's entrance. All other openings to the burrow system were blocked until the squirrel emerged into the trap. Trapped squirrels were weighed, marked with monel fingerling tags, and age (juvenile, yearling, or adult when these could be distinguished), sex,

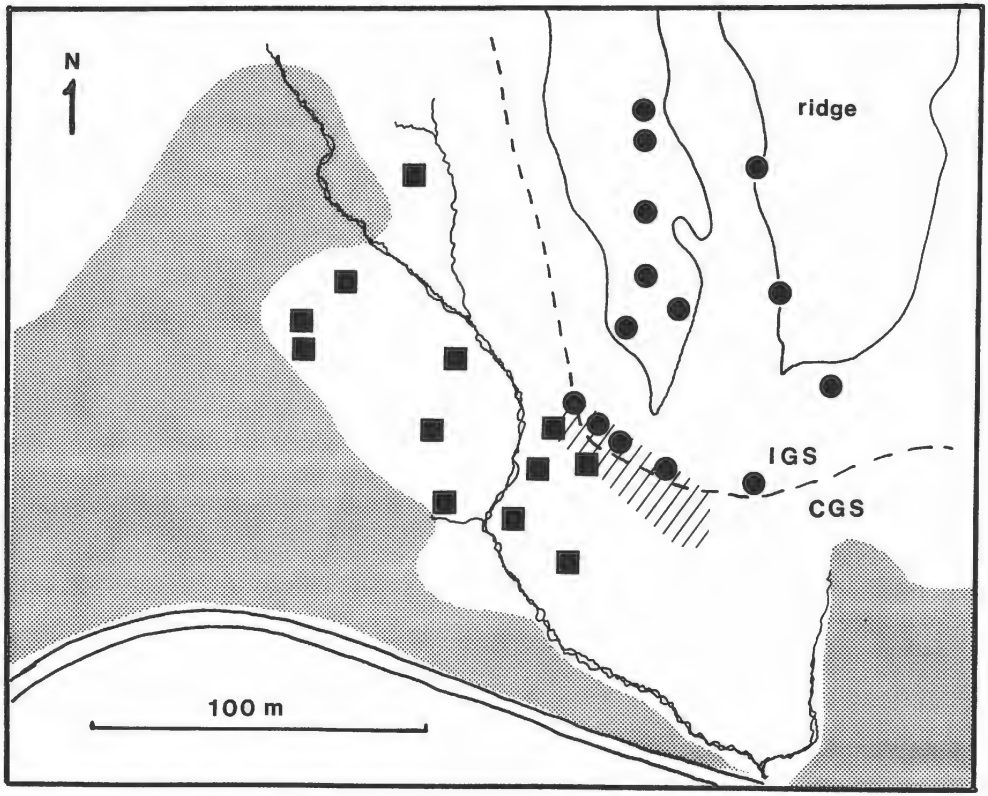

Figure 1. Map of Huckleberry study site, Adams Co., west-central Idaho showing capture locations of *Spermophilus brunneus* (circles) and *S. columbianus* (squares) for fecal pellet analysis. Cross-hatching indicates an area where both species foraged, although burrow locations were in areas separated by the dashed line; IGS = Idaho ground squirrel area, CGS = Columbian ground squirrel area. The shaded area indicates forested areas; forest also occurs south of the road, but is not shown. The two ridges (upper right) have shallow soils and xeric vegetation.

reproductive condition, and trap location were noted. Fecal pellets were collected from each animal and stored in paper envelopes with salt until processed. Voucher specimens of *S. brunneus* and *S. columbianus* were deposited in the Albertson College Museum of Natural History.

Fecal pellets were collected at Squirrel Valley on 9-17 June 1988 (soon after the pups were weaned) and at Huckleberry on 30 June-8 July 1988 (prior to onset of estivation of males). Huckleberry is at higher elevation and the growing season lags about two weeks behind Squirrel Valley (E. Yensen, unpublished data), but at the time of pellet collection the squirrels' active season at Huckleberry was about one to two weeks more advanced than when pellets were collected at Squirrel Valley. Both squirrel species have similar seasonal activity cycles, emerging from hibernation in late March or early April and reentering seasonal torpor in late July or early August, always within a few days of each other at a site (E. Yensen and P.W. Sherman, unpublished data).

We collected 181 herbarium sheets at Huckleberry and 97 at Squirrel Valley as part of a larger collection of 925 sheets from the general area. These specimens were deposited in the Harold M. Tucker Herbarium at Albertson College. Plant collections at the two sites were made between 28 March-7 August 1987, 26 March-30 July 1988, and 27 April-6 May 1989, and should be reasonably complete inventories of the species at each site.

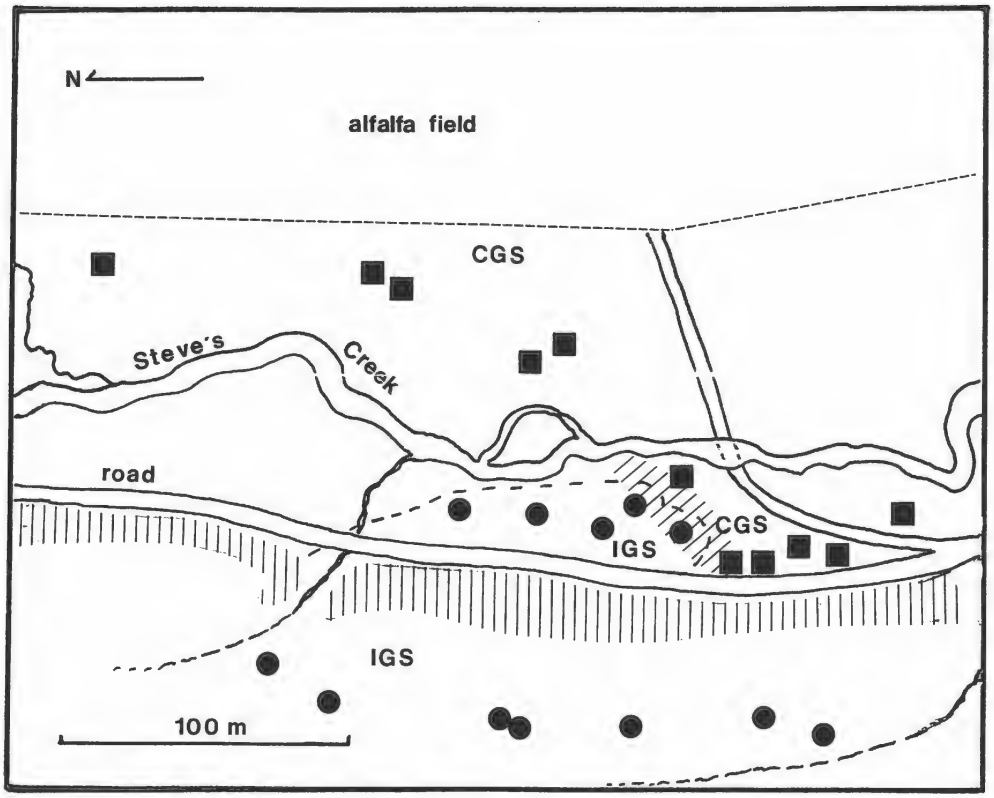

Figure 2. Map of Squirrel Valley study site, Adams Co., west-central Idaho showing capture locations of *Spermophilus brunneus* (circles) and *S. columbianus* (squares) for fecal pellet analysis. Cross hatching indicates an area where both species foraged, although burrow locations were in areas separated by the dashed line; IGS = Idaho ground squirrel area, CGS = Columbian ground squirrel area. Vertical hatching indicates a steep bank up to 8 m tall.

In the laboratory, each group of pellets from a single squirrel was soaked in water 5-15 min to remove salt, diluted with water, and homogenized 1 min in a Waring blender. Following Hansen's (1978) method, the homogenate was washed through a 1 mm sieve and collected below on a 0.1 mm sieve. A portion of the homogenate was placed on each of five microscope slides, cleared with Hertwig's solution, and mounted using Hoyer's medium (Sparks and Malechek 1968).

Plant species in the diet were identified using microhistological characters by comparisons to a collection of reference slides of leaves/stems, flowers, seeds, and roots. These were prepared from mounted, catalogued specimens in the Harold M. Tucker Herbarium at Albertson College using the technique above. The plant specimens used were collected at the study sites or in the general area, and the sheets were so annotated. Botanical taxonomy and nomenclature follows Hitchcock and Cronquist (1973).

Plant fragments in fecal samples were identified and categorized as leaves/stems, flowers, seeds, and roots/bulbs. Frequency of occurrence of food categories was recorded from 20 microscope fields per slide using a phase-contrast microscope at 100X. Five slides were examined per fecal cluster. Frequency of items in 100 fields was then converted to percent relative density (Sparks and Malechek 1968) using a table developed for frequency-to-density conversion (Fracker and Brischle 1944). Accuracy and precision of the

technique were calibrated using test slides with known mixtures of plant species found at the sites (Holechek and Gross 1982). Accuracy of identification of slide contents was >99% and precision of frequency of items averaged 90.9% (83-96%, s=4.02) in 35 tests.

After collecting the fecal pellets, vegetation at each site was sampled using a point frame method which measured cover at 36 points in a 0.5 x 1 m area (Floyd and Anderson 1987). Four to six transects were established which crossed each area where foraging squirrels had been captured (hereafter, Idaho ground squirrel area, Columbian ground squirrel area). Point frame sampling was done at 8-11 random intervals on each of the transects.

Dietary preferences were analyzed by comparison of a plant species' rank order of abundance in the diet with its abundance in the vegetation sampling. This was done for all species with >1% importance values in the vegetation analysis. However, we did not use Johnson's (1980) rank preference indices because of the large number of rare dietary categories which could not be reliably ranked.

Dietary and vegetation similarity were quantified using the Bray-Curtis similarity index (C=2w/a+b) with a computer routine provided in Ludwig and Reynolds (1988). SYSTAT 5.0 (Wilkinson 1990) was used for statistical analyses; $P<0.05$ was accepted as the level of statistical significance.

Results

Vegetation Analysis

We recorded 98 species of vascular plants from Squirrel Valley and 125 species from Huckleberry. Only 38 species occurred at both, a 34.1% similarity in species composition between sites.

At Squirrel Valley, the Columbian ground squirrel area was dominated by grasses (graminoid importance value = 70.4) with 96% total plant cover (Table 1). The Idaho ground squirrel area had fewer grasses (importance value = 56.2) but more forbs (42.1) and high total plant cover (91%). At Huckleberry, the contrast between Idaho and Columbian areas was greater. The Columbian area was again dominated by grasses (62.7) with 97% cover, while the Idaho ground squirrel area had fewer grasses (33.1) and less cover (59%).

At Squirrel Valley, the vegetation of areas occupied by *S. brunneus* and *S. columbianus* were more similar (52%) than at Huckleberry (13%). Correspondingly, the lush meadows used by Columbian ground squirrels at Huckleberry and Squirrel Valley were 37% similar, whereas the Idaho ground squirrel areas at the two sites were only 25% similar. Thus, the mesic areas used by *S. columbianus* were more similar to each other at the two sites than the xeric areas used by *S. brunneus*.

The Columbian ground squirrel areas were floristically less diverse. They had about half as many species in the vegetation analysis as areas occupied by Idaho ground squirrels (25 vs. 52 species for Squirrel Valley and 17 vs. 35 at Huckleberry). Point frame sampling found only one species (*Poa praetensis/compressa*) common to all four areas (Table 1).

Diet Analysis

We analyzed fecal pellets from 49 ground squirrels: 14 *S. brunneus* and 12 *S. columbianus* from Huckleberry and 12 and 11 individuals, respectively, from Squirrel Valley. Four *S. brunneus* and two *S. columbianus* from Huckleberry were sampled from the common foraging area, as were two of each species at Squirrel Valley (Figs. 1 and 2).

There were a minimum of 68 species belonging to 55 genera of plants in the fecal pellets of *S. brunneus* and *S. columbianus* at the two sites. Including the leaves/stems, flowers, seeds, and roots/bulbs of each species as separate categories, and adding insects, fungi, bryophytes, and *Equisetum* sp., we found a total of 141 food categories in the fecal pellets (Table 2; a complete list is available from the authors).

At Squirrel Valley, *S. columbianus* had a more diverse diet (74 categories and 58 plant species in the fecal samples) than *S. brunneus* (55 categories and 45 plant species). Leaves of two bunch grasses, *Poa bulbosa* and *Bromus commutatus/tectorum,* were important for both species, as were Asteraceae seeds, and leaves of lupine and alfalfa (Table 2).

At Huckleberry, each species of squirrel consumed 75 dietary categories, consisting of a minimum of 50 and 52 plant species for *S. brunneus* and *S. columbianus*, respectively (Table 2). Seeds

TABLE 1. Vegetation analysis of areas used by Idaho (IGS) and Columbian ground squirrels (CGS) at two study sites in Adams Co., Idaho. Data are importance values from point frame sampling. Species with importance values <1 are not listed, but are included in totals.

	Squirrel Valley		Huckleberry	
Species	IGS	CGS	IGS	CGS
Agropyron cristatum	2.59	—	—	—
Agropyron intermedius	3.78	14.60	—	1.40
Agropyron spicatum	—	1.64	—	—
Agrostis tenuis	—	—	5.51	—
Bromus commutatus	2.92	1.86	2.12	—
Bromus inermis	2.36	10.09	4.82	—
Festuca ovina	3.65	—	—	—
Koeleria nitida	1.12	—	—	—
Phleum pratense	4.64	—	—	—
Poa praetensis/compressa	13.57	27.49	3.66	14.22
Poa bulbosa	8.44	10.63	4.71	—
Poa scabrella	—	—	4.61	—
Poa sp.	3.76	—	—	—
Stipa columbiana	—	3.06	2.80	25.14
Sitanion jubatum	1.12	—	—	—
Carex spp.	—	0.81	—	14.09
Juncus spp.	4.13	—	2.51	7.09
Total Graminoids	56.22	70.39	33.06	62.65
Achillea millefolium	1.80	1.52	6.36	—
Allium tolmiei	—	—	1.83	—
Antennaria spp.	2.17	—	4.72	—
Balsamorhiza sp.	1.97	—	—	—
Cirsium spp.	—	0.92	—	1.58
Clarkia pulchella	1.31	—	—	—
Erigeron pumilus	—	—	—	3.87
Erigeron sp.	2.42	2.07	—	—
Eriogonum heracleoides	—	—	—	6.18
Eriogonum sphaerocephalum	—	—	7.64	—
Eriogonum umbellatum	—	—	4.05	—
Frasera albicaulis	1.11	—	1.26	—
Gayophytum diffusum	—	—	7.31	0.89
Geranium viscosissimum	—	3.84	—	4.58
Lomatium grayi	—	—	9.76	—
Lupinus laxiflorus	2.72	—	—	—
Lupinus leucophyllus	1.43	0.94	—	—
Madia gracilis	—	—	1.44	—
Microseris sp.	1.68	—	—	—
Navarretia intertexta	—	—	1.44	—
Penstemon spp.	—	—	—	2.11
Potentilla glandulosa	0.87	—	1.54	—
Potentilla gracilis	14.26	12.16	0.77	11.95
Potentilla recta	—	—	5.41	2.80
Potentilla sp. seedlings	—	—	3.68	—
Sedum stenopetalum	—	—	1.83	—
Sidalcea oregana	1.11	0.48	3.65	—
Spergularia rubra	—	—	—	2.03
Taraxacum spp.	—	—	—	0.71
Total forbs	42.11	24.85	65.40	37.41
Symphorocarpus oreophilus	—	2.52	0.48	—
Total shrubs	1.73	2.94	0.48	—
Equisetum sp.	—	1.88	—	—
moss	—	—	1.07	—
Total non-vascular	—	1.88	1.07	—
TOTAL	100.06	100.06	100.01	100.06
Total cover (%)	91.23	96.42	59.03	97.05
Total species	52	25	35	17

TABLE 2. Food categories comprising >1% of diet of Idaho ground squirrels (IGS) and/or Columbian ground squirrels (CGS) at two study sites in Adams Co., Idaho. Symbols: + = <0.1%., lv = leaves, st = stems, fl = flowers. Because of omitted categories, totals may be higher than sum of amounts shown in table. A complete list of dietary categories is available from the authors.

	Huckleberry (early July)		Squirrel Valley (early June)	
Food Category	IGS	CGS	IGS	CGS
n	14	12	12	11
Agropyron lv	0	0	0	5.6
Bromus commutatus/tectorum lv	0.5	0	7.7	12.3
Bromus sp. fl/seed	1.5	0.9	0	0.3
Danthonia californica fl/seed	1.9	0	0	0
Poa bulbosa fl	1.9	0.9	21.4	19.6
Poa pratensis lv	0	8.0	1.5	4.0
Poa sp. lv	0.6	+	0	1.0
Poa sp. fl	+	0.9	2.8	0.4
Stipa sp. seed	17.4	55.3	0	+
grass fl	2.0	0	0	+
Carex sp. fl/seed	+	2.0	0	0
TOTAL GRAMINOIDS	26.3	68.4	34.7	43.5
Allium sp. lv	+	+	2.3	0
Allium sp. seed	2.0	+	0	0
Calochortus eurycarpus seed	0	0	1.9	0
TOTAL OTHER MONOCOTS	3.1	+	4.2	0
Achillea millefolium lv/fl	0	0	0	1.2
Artemisia arbuscula lv/fl	0	0	0	1.0
Artemisia ludoviciana lv	0	0	0	2.2
Erigeron pumilis lv/st	0	0.6	1.2	0.9
Madia sp. seed	5.9	+	0	0
Microseris nigrescens lv/st	0	0	13.9	0.2
Tragopogon dubius seed	0	0	4.0	+
Asteraceae seed	0.4	0.6	8.7	5.9
Cryptantha sp. lv	0.2	0.1	+	1.3
Cryptantha sp. seed	13.6	0.4	+	0
Plagiobothrys scouleri seed	3.5	0	0	0
Descurainia sp. lv/st	+	+	0.1	1.2
Scrophulariaceae seed 1*	9.1	0	+	0
Polygonaceae? lv	0.5	0.1	0	2.0
Collomia linearis fl/st	0	0	1.0	0
Collomia linearis seed	0.6	1.2	0	0.1
Gilia aggregata seed	3.9	0.3	0	0
Microsteris nutans lv/st	0.2	0	1.8	+
Microsteris nutans seed	2.0	0.8	1.0	1.7
Polemoniaceae seed	1.4	2.8	0	0
Amelanchier alnifolia lv	0.3	1.8	0	0
Potentilla/Fragaria seed	0	1.8	0	+
Viola sp. lv/st	+	1.4	0.2	0.5
Lupinus sp. lv/st	0	5.9	9.3	4.4
Lupinus sp. fl/seed	0	+	+	8.6
Medicago sp. lv/st	0	0	7.3	13.2
Lomatium sp. seed	4.5	0.3	0	0
Silene menziesii lv/st	0	0.2	0	1.4
unk 2 lv	0	0	1.3	0.8
unk 3 root	0	0.4	1.4	0.2
unk 4 root/stem/bulb	11.6	0.1	1.8	+
unk 5 root/stem	0	0	1.5	0
unk 7 seed	2.8	+	+	0
unk 22 dicot tissue	1.2	0	0	0
TOTAL DICOTS	66.2	26.1	56.1	55.7
insects	4.3	5.4	5.1	0.7
TOTAL MISC.	4.4	5.4	5.2	0.7
TOTAL	100.0	100.0	100.0	100.0

**Castelleja* sp., *Orthocarpus* sp., and/or *Penstemon* sp.

of needlegrass (Stipa sp.) were the only food category utilized heavily by both species (Table 2).

The diets of the two species were more similar to each other at the vegetatively more homogeneous Squirrel Valley (52%) than at Huckleberry (30%). *S. brunneus*' diet was only 10% similar between sites whereas *S. columbianus*' diet was 15% similar.

Although both species of ground squirrels at both sites ate a large number of food categories, most were present in small quantities. For example, at Huckleberry, Idaho ground squirrels ate 75 categories of foods, but only 18 comprised >1% of the diet, and only 5 comprised >5% of the diet (Table 2). The patterns for Columbian ground squirrels at Huckleberry and both squirrels at Squirrel Valley were similar, although Idaho ground squirels tended to have more food sources comprising >1% of the diet (18 and 20) than Columbian ground squirrels (10 and 17). Only 44 of the 141 (31%) of the food categories were shared between Squirrel Valley and Huckleberry.

Although the details were different, the two squirrels consumed similar sets of dietary categories at Squirrel Valley in early June. Leaves/stems were most important, followed by flowers and seeds. At Huckleberry in late June-early July, both squirrels also used similar dietary categories, although Idaho ground squirrels ate more seeds, roots/bulbs, and fewer leaves/stems, than Columbian ground squirrels (Table 3).

Within a species at the same site, fecal pellet content varied considerably from squirrel to squirrel. Food categories sampled from individual squirrels varied from 0 to 83% ($\bar{X}$=34.3%) similar. Content of fecal pellets of individual *S. columbianus* was most similar at Huckleberry (60%) and most dissimilar at Squirrel Valley (25.4% similarity), whereas similarity among *S. brunneus* individuals was low at both sites (27.1% similarity at Huckleberry and 34.1% at Squirrel Valley).

Rank order comparisons of ground squirrel diets with plant abundance at each site indicated that although the squirrels fed in small amounts upon many plant species at each site, they were selective feeders. There was no correlation (Spearman r_s = 0.086, P>0.5) between a plant species' rank in the vegetation analysis and its rank in the diet. Although several plant species were common in the diets, most of these were rare in the habitat, and many were too rare to appear in the vegetation analysis. Of the 44 species in the diets, half (22) had ranks >25 in the vegetation analysis.

TABLE 3. Major patterns of resource utilization (percentage use) by Idaho (IGS) and Columbian ground squirrels (CGS) at two study sites in Adams Co., Idaho.

	Huckleberry (early July)		Squirrel Valley (early June)	
Category	IGS	CGS	IGS	CGS
Leaves/stems	3.4	24.4	47.8	57.9
Flowers	5.4	2.0	24.3	30.1
Seeds	73.6	67.7	18.0	9.6
Roots/bulbs	13.2	0.5	4.7	0.2
Insects	4.3	5.4	5.1	0.7
Non-vascular plants	0.1	0.0	0.1	1.5
TOTAL	100.0	100.0	100.0	100.0

Discussion

Vegetation analysis confirmed what was apparent to the eye: Columbian ground squirrels inhabit areas with more luxuriant vegetation. Either squirrel may be able eat plants in the area occupied by the other species, but the low density of food resources may make it unprofitable for *S. columbianus* to attempt to maximize energy intake (Belovsky and Schmitz 1994) in more xeric areas, leaving those areas open to exploitation by *S. brunneus* with one-third the body mass. In addition, the shallower soils in the xeric areas may not allow enough depth for Columbian ground squirrel burrows. Foraging at a distance from a burrow should increase the risk of predation for a ground squirrel. Thus, the larger Columbian ground squirrels would have higher energetic requirements and should forage more efficiently and safely in more productive habitats.

There was no indication of unique dietary specialization in *S. brunneus* which would suggest reasons for its rarity. Idaho ground squirrels ate 45 and 50 species of plants at the two study sites, and the dietary categories differed more between sites than between ground squirrel species.

Idaho and Columbian ground squirrels appear to select the same types of food resources. Of the 49 food categories that comprised >1% of the diet, 37 (75%) were consumed by both species, despite the differences in plant composition of the areas and limited sample sizes. Further, the dietary

similarities within and between species and sites paralleled vegetation similarities, indicating that more similar resources were consumed when they were available.

The dietary differences between species thus appear to be the result of food plant availability in xeric vs. mesic meadows rather than inherent dietary preferences. Small pockets of mesic vegetation in the xeric areas gave Idaho ground squirrels access to nearly all of the species available to Columbian ground squirrels, although the amounts were different. With one exception at Squirrel Valley, xeric areas were no more than 100 m from the burrow of any Columbian ground squirrel captured, so they would thus have access to the resources there.

The growing season was about two weeks later at Huckleberry than Squirrel Valley because of elevation, but sampling at Huckleberry was done three to four weeks after Squirrel Valley. This time difference should not have affected the vegetation analysis, but the xeric areas at Huckleberry were already drying out by late June when green vegetation would have been losing its nutritional value (Murray et al. 1978), but more seeds were available. This may explain the higher proportion of seeds consumed at Huckleberry. Thus, the dietary differences between sites was due partly to season and partly to species composition. Idaho ground squirrels ate more dicot seeds, roots and bulbs whereas *S. columbianus* ate more dicot leaves, grass seeds and flowers, and grass leaves at Huckleberry, but these foods are green longer in wet meadows (E. Yensen, unpubl. data). Lambeth and Hironaka (1982) and Elliott and Flinders (1985) found that Columbian ground squirrel diets varied considerably from one site to another, sometimes with little overlap among sites.

Both species concentrated on a few important species, and also ate a little of a great many species. Given the high degree of individual dietary variation (34% similarity), our sample sizes were too small to determine if the differences among particular squirrels reflected individual dietary preferences, or were simply an artefact of the sampling process. However, like other studies of ground squirrel diets (e.g., Fitch 1948, Hansen and Johnson 1976, Yensen and Quinney 1992), we did not find any sex- or age-related differences in resource utilization patterns.

In summary, we found broad dietary overlap between *S. brunneus* and *S. columbianus* suggesting that the two are competitors for the same food resources. Because of its larger body size, we would expect *S. columbianus* to win any aggressive encounter and thus restrict *S. brunneus* to less productive sites not used by *S. columbianus*. However, many less productive sites lack pockets of deep, well-drained soils (pers. obs.) needed for nest burrows (Yensen, et al. 1991), limiting the number of sites that could be occupied by *S. brunneus*. Thus, dietary overlap with *S. columbianus* suggests that competition could be an important factor in *S. brunneus*' rarity.

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Amphibian and Reptile Abundance in Riparian and Upslope Areas of Five Forest Types in Western Oregon

Abstract

We compared species composition and relative abundance of herpetofauna between riparian and upslope habitats among 5 forest types (shrub, open sapling-pole, large sawtimber and old-growth conifer forests, and deciduous forests) in Western Oregon. Riparian- and upslope- associated species were identified based on capture frequencies from pitfall trapping. Species richness was similar among forest types but slightly greater in the shrub stands. The abundances of 3 species differed among forest types. Total captures was highest in deciduous forests, intermediate in the mature conifer forests, and lowest in the 2 young coniferous forests. Species richness was similar between stream and upslope habitats; however, captures were higher in riparian than upslope habitat. Tailed frogs (*Ascaphus truei*), Dunn's salamanders (*Plethodon dunni*), roughskin newts (*Taricha granulosa*), Pacific giant salamanders (*Dicamptodon tenebrosus*) and red-legged frogs (*Rana aurora*) were captured more frequently in riparian than upslope habitats. Of these species the red-legged frog and Pacific giant salamander may depend on riparian habitat for at least part of their life requirements, while tailed frogs, Dunn's salamanders and roughskin newts appear to be riparian associated species. In addition, we found Oregon salamanders (*Ensatina eschscholtzi*) were associated with upslope habitats. We suggest riparian management zones should be at least 75-100 m on each side of the stream and that management for upslope/and or old forest associates may be equally as important as for riparian species.

Introduction

Much riparian management in the Pacific Northwest has been focused on protection of fish habitat along larger streams (Meehan et al. 1977, Sedell et al. 1981). Bilby (1988) suggested that the alterations along the smaller streams have a more dramatic effect than on larger streams, because they shift the primary source of organic matter from land to the stream. Leopold et al. (1964) estimated that 85 % of the total length of running waters are first- to third- order streams. Changes in these streams may alter the structure and productivity at higher levels of the riparian food chain (Murphy and Hall 1981, Hawkins et al. 1983), and eventually may drastically effect riparian-associated plants and animals, some which are already listed by the Department of Interior as threatened or endangered (Hirsch and Segelquist 1978).

Intergradation of riparian vegetation with the adjacent upland habitat provides increased structural diversity of vegetation for wildlife (Thomas et al. 1979), and amphibians and other vertebrates have an important role in the food chain of these ecosystems (Bury et al. 1980, Brode and Bury 1981). The cool-moist microclimate found in riparian habitats may be essential for some herpetofauna, and it undoubtedly offers limited resources to others during at least part of the year (Brode and Bury 1981). Riparian habitat is used by many amphibians for cover and/or breeding habitat (Bury 1988). Alterations in these components by changes in the forest can be detrimental to many amphibian species, including salamanders (Bury et al. 1980). Increased temperatures of exposed stream-beds as a result of timber removal were hypothesized to lead to the disappearance of the tailed frog (Bury 1968; Noble and Putnam 1931). Bury and Corn (1988) suggested that canopy removal may negatively effect the tadpole population of tailed frogs by increasing water temperatures and altering the food base. Brode and Bury (1981) found that populations of Torrent salamanders (*Rhyacotriton variegatus*), which are often associated with cool ravines and rivulets, were eliminated by logging in Northwestern California. Although the numbers of herpetofauna species in the Pacific Northwest is lower than birds and mammals, their ecological significance as measured by density and biomass is high (Bury 1988). Thomas et al. (1979) suggested that vertebrates which feed and/or reproduce in water are usually dependent on riparian habitat, but some amphibians including the plethodontid salamanders, have a less direct association with water and are more general in their habitat requirements.

Life history information is available for some herpetofauna in the Oregon Coast Ranges

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(Nussbuam et al. 1983). Ten of 24 native species of herpetofauna in the Oregon Coast Ranges often are found in riparian habitat (Marshall 1986). Bury (1988) indicated that the northwestern salamander (*Ambystoma gracile*) and the roughskin newt require water (preferably slow moving) for breeding. He also stated that the northern alligator lizard (*Elgaria coerulea principis*) may be more abundant along the streams, but it does not require riparian habitat for survival. Bury (1988) concluded that none of the herpetofauna of the Oregon Coast or Northern California appear to be riparian obligates, because none of them are dependent on riparian habitat alone for both breeding and cover. His statement left some doubt about the occurrence of riparian obligate herpetofauna in the Oregon Coast Ranges.

The purpose of this study was to describe differences in species composition and relative abundance of herpetofauna between riparian and upslope habitats among five forest types. Our primary objective was to identify any species with riparian or upslope associations in order to develop management strategies for these species.

Methods

Study Sites

Fifteen study sites were located in the Central Coast Ranges, Lincoln County, Oregon along second-, third-, and fourth-order streams (Horton 1945; Strahler 1957) (Figure 1). "Stream Order" is a system of stream classification; each small unbranched tributary is a first-order stream; two first order streams join to make a second-order stream; a third order stream has only first- and second-order tributaries, etc. (Brown 1985:201). The Coast Ranges is influenced by the maritime climate of Western Oregon, with mild-wet winters and cool-dry summers (Brown and Curtis 1985). The annual precipitation ranges from 64 cm in the interior valleys to 305 cm on the western slopes of the coastal mountains (Brown and Curtis 1985). Franklin and Dyrness (1973:31-32) described the Coast Ranges as a narrower zone which receives 170-300 cm of precipitation a year, with average temperatures that seldom drop below 0°C in the winter and never exceed 27°C in the summer. The upland soils of these areas consist largely of silt loams and clays (of sedimentary origin) and finer textured clay loams which are igneous (Maser et al. 1981). Organic matter content is high and acidity is medium (Franklin and Dyrness 1973:9-10). There may be substantial differences in soil types which occur locally as topography changes from poorly developed soils on steep slopes to deep soils on gradual slopes (Maser et al. 1981).

We selected study sites in five forest types (Hall et al. 1985) including: (1) shrub conifer forests; 5-10 years old, trees <3 m tall, dbh <2.5 cm, <40%

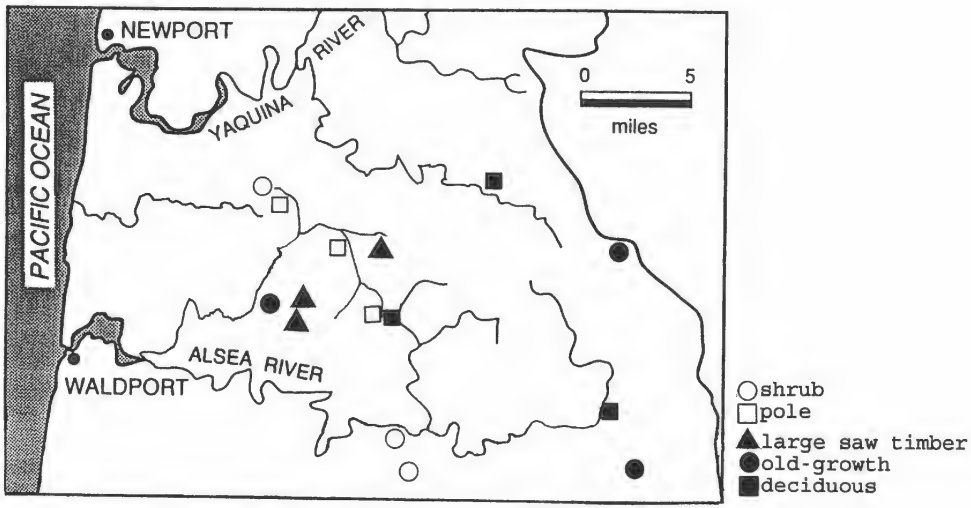

Figure 1. Map of study site locations, Lincoln County, Oregon.

crown cover, with grass-forb condition intermittent, dominant tree species Douglas-fir (*Pseudotsuga menziesii*) (2) open sapling-pole conifer forests; 20-35 years old, trees usually >3 m tall, 2.5-10 cm dbh, <60% crown cover, dominant tree species Douglas-fir (3) large sawtimber conifer forests; 110-200 years old, trees usually >30 m tall, dbh >53 cm, 60-80% crown cover, dominant tree species Douglas-fir 4) old-growth conifer forests; 200+ years old, multilayered vertical structure, 60-80% crown cover, dominant tree species Douglas-fir and western hemlock (*Tsuga heterophylla*) and 5) deciduous forests; >70% cover, dominant tree species, red alder (*Alnus rubra*) and bigleaf maple (*Acer macrophyllum*). Forest type selection was based on a combination of age, species and structural characteristics, and was limited to what was available in the Oregon Coast Range. We sampled three replicates of each forest type (= 15 total stands). Each stand had the appropriate forest type on both sides of the stream and was large enough to include the transects plus a buffer of at least 100m to reduce edge effects. Aerial photos and field reconnaissance were used to locate sites. The elevation of the study sites ranged from 110-378 m and slope was from 28 to 68%. Aspect, slope, litter depth and other habitat variables were measured at each station at each site (Gomez 1992).

Trapping Design and Method

Transect lengths and spacing between trap stations were modified from McComb et al. (1991), these reductions allowed us to maximize the efficiency of the study design and the search for study sites, but still obtain a representative sample of the population. The trapping design on each study site consisted of one 350-m riparian transect, one 350-m upslope transect (200 m upslope and parallel to the riparian transect), and two 200-m trans-riparian transects that connected the ends of the riparian and upslope transects (Figure 2). Eight trap stations with two pitfall traps/station were located at 50-m intervals along the riparian and upslope transects and nine trap stations at 25-m intervals along the trans-riparian transects. There were 60 pitfall traps per stand and a total of 900 traps for all stands combined. Multiple traps were used per station to increase capture rates. The traps were constructed by taping two #10 sized cans together and placing them in holes so that the top of the can was flush with the ground. Traps were located within a 10 m radius of the station center

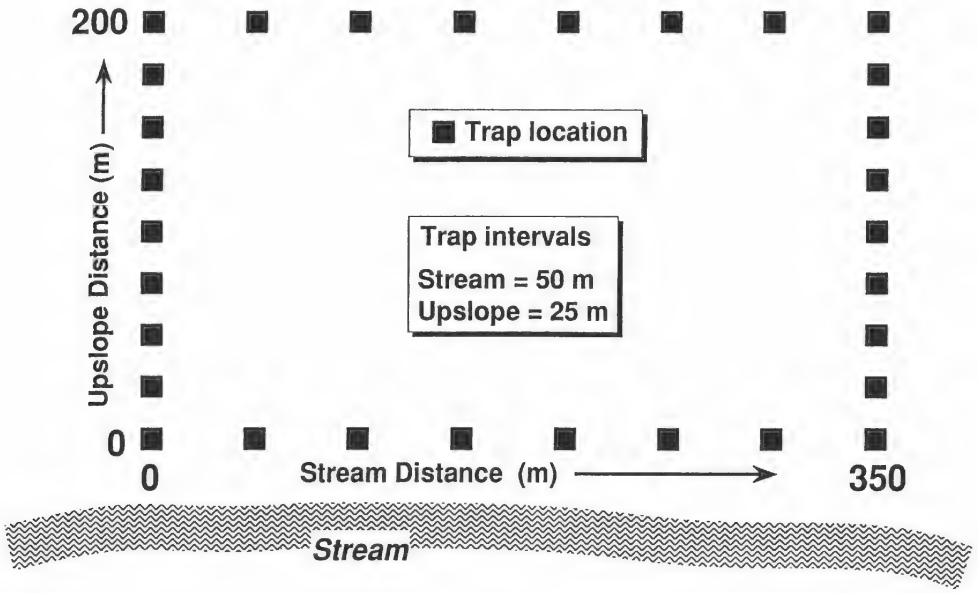

Figure 2. Study site design for placement of pitfall traps.

to allow trap placement along fallen logs, stumps, live trees, rocks, or slope breaks, which acted as natural drift fences. Kill trapping methods were used in this study because of poor accessibility to the sites and time constraints.

The study included four 28-day trapping periods during May (cool, wet season) and August (hot, dry season) of 1989 and 1990. Each trap was checked weekly which resulted in 100,800 trap nights. Dead animals were taken from the field to freezers where they were stored for positive identification. Live animals were identified and released in similar habitats at an adequate distance (miles) outside the study sites to prevent recapture.

Data Analysis

All data analysis was conducted using the SAS software system (SAS Institute 1987). Relative abundance of each species was compared among forest types using one-way Analysis of Variance (ANOVA) and Student-Newman-Kuels (SNK) mean comparison test. Relative abundance of each species was compared between stream and upslope habitats among forest types, and stations along the trans-riparian gradient among forest types using two-way ANOVA and Student-Newman-Kuels (SNK) mean comparison test. SNK was chosen for its power in declaring significant differences and because it works well with equal sample sizes. The transect by forest type interaction and station by forest type interaction were used to test the transect effect and station effect along the trans-riparian gradient, respectively. Site within forest type was used as an error term when the interaction between transect and forest type (or station and forest type) was insignificant. When the mean square for site within forest type was less than the mean square for transect by site within forest type, the site within forest type error term was dropped and it became a completely randomized design. This procedure allowed us to separate the effects due to differences among forest types and sites from differences between and within transects. When necessary, variables were transformed [log10 (x+1) and arc sine square-root for percent cover] to correct for non-normality or to obtain homogeneous variances. In some cases transformations were unsuccessful in producing normally distributed variables or homogeneous variables. Comparisons were made among habitats and between transects for each species individually. Results for some species were not included, because small sample sizes (N<20) made statistical analysis and interpretations tenuous.

Results

Abundance and Species Richness

A total of 917 amphibians and reptiles were captured including nine species of amphibians and three species of reptiles (Table 1). Amphibian species richness was greatest in the pole forest type (9 species) and slightly lower in the old-growth forests with six different species. Reptile species richness was greatest in the shrub forest type (3 species) and only one species was found in the other forests types. Species richness was similar in stream (8 amphibian and 3 reptile species) and upslope (9 amphibian and 2 reptile species) habitats with 11 species each (Table 2). Amphibian abundance was highest in the deciduous forest type, intermediate in large sawtimber and old-growth forest types, and lowest in the shrub and pole timber forest types. In contrast, reptile abundance was highest in the shrub forest type. Amphibian abundance was greater in the riparian than upslope habitats, and reptile abundance was greater in upslope habitats (Table 2). The species capture rate was similar between seasons along riparian and upslope transects; there were no significant differences in capture rates between wet and dry seasons for any species.

There was a total of 858 amphibians captured, which included seven salamander and two frog species. The roughskin newt, tailed frog and western red-backed salamander (*Plethodon vehiculum*) together made up 82% of the amphibians and 76% of the total herpetofauna (Table 1).

The roughskin newt was the most abundant salamander in this study representing about 86% of the 350 salamanders captured. It was captured more often ($P<0.01$) along stream than upslope habitats (Table 2). Along the trans-riparian transects there was more captures at stations close to the stream than further away ($P<0.05$) (Figure 3). There was progressively fewer captures of roughskin newts from old to younger coniferous forests; however roughskin newts were more abundant in the deciduous forest type than in any of the other forest types (Table 1).

The Pacific giant salamander was captured more often ($P<0.05$) in the large sawtimber and old-growth

TABLE 1. Frequency of herpetofaunal captures among the five different forest types in the Oregon Coast Ranges, 1989-1990.

	Forest Type[a]											
	S (n=3)		P (n=3)		L (n=3)		O (n=3)		D (n=3)		Total	
Herpetofauna	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	Captures	P[b]
Amphibians:												
Northwestern salamander	0.0	0.0	0.7	0.7	0.0	0.0	0.0	0.0	1.0	1.0	5	—
Pacific giant salamander	0.3	0.3b	1.3	1.3ab	6.0	1.5a	4.7	2.7ab	1.0	0.0ab	40	0.0424*
Oregon salamander	2.3	0.7	4.3	1.7	4.7	0.9	5.0	2.6	5.7	1.5	66	0.6709*
Dunn's salamander	0.3	0.3	2.0	0.6	2.0	0.6	2.3	1.2	2.0	1.5	26	0.4833*
Red-backed salamander	10.7	4.8ab	6.0	1.5b	12.3	4.5ab	9.7	2.4ab	27.7	6.1a	199	0.0355
Torrent salamander	0.7	0.7	0.3	0.3	0.3	0.3	0.0	0.0	0.0	0.0	4	—
Roughskin newt	1.0	0.6b	7.0	3.6ab	10.7	5.8ab	17.7	11.8ab	64.0	22.5a	301	0.0620*
Tailed frog	1.0	0.6	2.0	1.0	29.7	3.5	25.0	21.6	9.3	5.2	201	0.0573*
Red-legged frog	1.3	1.3	0.3	0.3	0.0	0.0	0.0	0.0	3.7	3.2	16	0.4026*
Subtotals	53		72		197		193		343		858	
Reptiles:												
Northern alligator lizard	14.3	3.8a	1.7	0.9b	0.3	0.3b	0.3	0.3b	0.0	0.0b	50	0.0002*
Northwestern garter snake	1.7	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5	—
Common garter snake	1.3	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4	—
Subtotals	52		5		1		1		0		59	
TOTAL CAPTURES[c]	105		77		198		194		343		917	

*Variable was Log10 + 1 transformed.

Letters (a and b) are used to distinguish between means with significant differences. Significantly different means will not share the same letter.

[a]S=shrub, P=pole, L=large saw timber, O=oldgrowth, D=deciduous.

[b]2-way ANOVA with site as block and error term to test for stand-type effect. Letters represent specific differences identified by the multiple comparisons test.

[c]Not including non-target species and the specimens which were in too poor condition to identify.

TABLE 2. Frequency of herpetofaunal captures among the stream and upslope transects in five forest types in the Oregon Coast Ranges, 1989-1990.

	Transect					
	Stream (n=15)		Upslope (n=15)			
Herpetofauna	$\bar{X}$	SE	$\bar{X}$	SE	Total	P[a]
Amphibians:						
Northwestern salamander	0.1	0.1	0.1	0.1	2	—
Tailed frog	6.6	2.3	1.6	0.7	123	0.0033*
Pacific giant salamander	1.0	0.4	0.3	0.2	22	0.1211*
Oregon salamander	0.0	0.0	2.0	0.4	30	0.0003*
Dunn's salamander	1.1	0.3	0.3	0.1	20	0.0355*
Western red-backed salamander	3.2	0.6	3.4	0.9	99	0.6007*
Red-legged frog	0.8	0.6	0.1	0.1	14	0.0828*
Torrent salamander	0.2	0.1	0.1	0.1	4	—
Roughskin newt	7.3	2.6	2.9	1.2	153	0.0041*
Subtotals	305		162		467	
Reptiles:						
Northern alligator lizard	0.3	0.3	1.1	0.6	21	0.0619*
Northwestern garter snake	0.1	0.1	0.0	0.0	1	—
Common garter snake	0.1	0.1	0.1	0.1	3	—
Subtotals	8		17		25	
TOTAL CAPTURES[b]	313		179		492	

*Variable was Log10 + 1 transformed.

[a]2-way ANOVA with transect by stand condition interaction used to test for transect effect and site by condition used as error term.

[b]Not including non-target species and the specimens which were in too poor condition to identify.

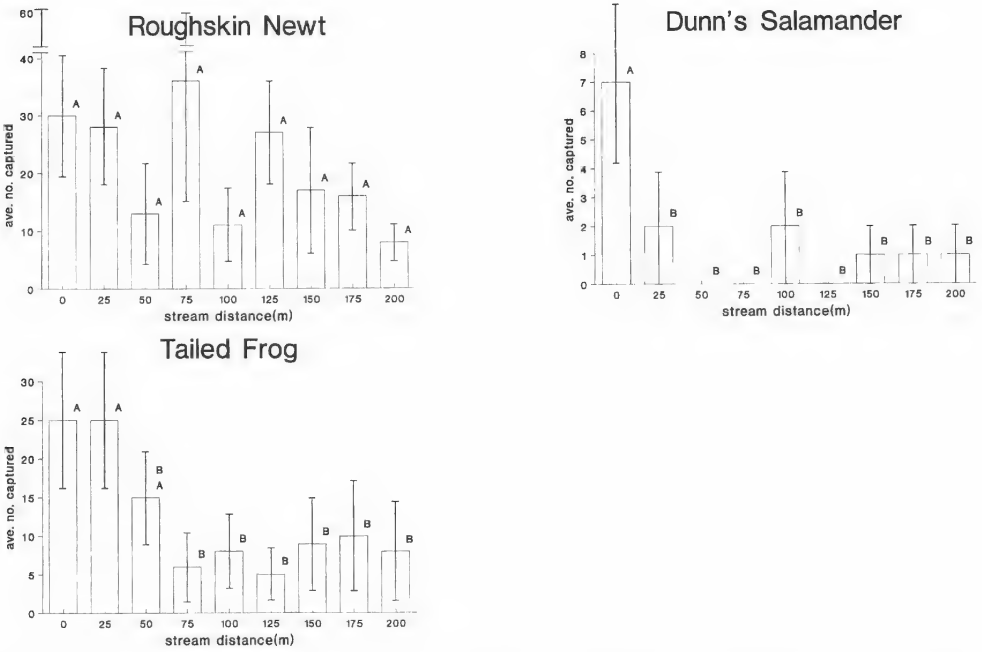

Figure 3. Average number of roughskin newts, Dunn's salamanders, and tailed frogs captured (±standard error) along trans-riparian transects (n=15) in the Oregon Coast Ranges, 1989-90. Letters (A and B) are used to distinguish between means with significant differences. Significantly different means will not share the same letter.

stands than in the other three forest types (Table 1) and was more abundant along the riparian than upslope transects (Table 2).

The Dunn's salamander was more abundant ($P<0.05$) in riparian than upslope habitats and was more abundant ($P<0.05$) at stream stations than stations away from the stream along the trans-riparian transects (Figure 3). Dunn's salamanders had a similar capture rate in all the forest types with the exception of the shrub stands where there was only one capture (Table 1).

The western red-backed salamander was more abundant in the deciduous than in the other forest types and least abundant in the pole forest type ($P<0.04$)(Table 1). It was the most abundant of the Plethodontids and comprised 68% of the total captures for the family.

The Oregon salamander was more abundant ($P<0.001$) in the upslope than riparian habitats (Table 2). In fact, there were no captures of this species in the riparian habitat in our study.

The tailed frog was more abundant ($P<0.01$) in the riparian than upslope habitats (Table 2) and was captured more frequently ($P<0.001$) next to streams compared to upslope habitats (Figure 3). Tailed frogs were found in all forest types in this study; however, it was more abundant in the large sawtimber and old-growth forest types than the other forest types (Table 1).

The red-legged frog was represented only by 16 individuals. It was more abundant in the deciduous stands than the other forest types and had higher captures in the riparian than upslope transects in this study.

There were 59 captures of reptiles, comprised of two snakes and one lizard species. Northern alligator lizards accounted for 85% of the reptiles but only 5% of all the herpetofauna. The northern alligator lizard was more abundant ($P<0.001$) in the shrub forest type than the other forest types. There were no captures of alligator lizards in the deciduous forests and only one capture in the large sawtimber and old-growth forests (Table 1). The

northern alligator lizard was more abundant in the upslope than stream habitat (Table 2).

Discussion

Salamanders

Dicamptodon is a genus endemic to moist coniferous forests of the Pacific Northwest, but the degree to which these species depends on aquatic environments is variable among the family (Nussbaum et al. 1983). The Pacific giant salamander depends on streams for breeding, and paedogenic forms require stream habitat for survival. However, transformed adults may be found on the forest floor under woody debris or fully exposed, especially during the rainy season (Nussbaum et al. 1983). In this study, the Pacific giant salamander was significantly more abundant in large sawtimber and old-growth forests than in the other three forest types and was more abundant along the riparian than upslope transects. Only 10 % of the Pacific giant salamanders captured in this study, were in young (< 35 yr.) coniferous forests. Similarly, McComb et al. (1993) captured more Pacific giant salamanders on streamside compared to upslope transects but the differences were not statistically significant. Raphael (1984) and Bury and Corn (1991) also found the Pacific giant salamander to be more abundant in mature coniferous forests than in young coniferous forests. Bury (1983) compared logged and unlogged redwood forests and found Pacific giant salamanders absent from the former. Our results support those of previous studies, and we suggest that changes in microclimate and vegetation for 35 or more years following a clear-cut may make areas unsuitable for Pacific giant salamander populations.

The genus *Taricha* is the only newt genus in western North America, and the roughskin newt is the only species found in the Pacific Northwest. The roughskin newt is the most common salamander in the Pacific Northwest and may be found in numerous habitats including coniferous and hardwood forests, open valleys and farmlands (Nussbaum et al. 1983). In this study, the roughskin newt was captured more often along streams than upslope habitats and there were differences in number of captures at stations along the transriparian gradient. McComb et al. (1993) found little difference in capture rate between stream and upslope habitats of mature coniferous forest for the roughskin newt. These results do not differ from this study; captures of the rough-skinned newt were low in the large saw timber stands with 6 individuals found in both the upslope and riparian transects. Eighty-three percent of roughskin newt captures in upslope and riparian transects were in the deciduous and old-growth stands in this study, although these differences among forest types were not statistically significant. This species may be restricted to low gradient sections of creeks and streams during breeding (Bury and Corn 1991). However, Nussbaum et al. (1983) suggested they may also be found in lakes, ponds, and on land. Similar to this study, Corn and Bury (1990) found roughskin newts more frequently in old-growth than in younger conifer stands, and Raphael (1984) found greater abundance of roughskin newts in mature conifer stands than in younger (<150) and older (>250) conifer forests. The roughskin newt was most abundant in the deciduous forest type in this study and we suggest from our results that it might benefit from management which includes maintenance of some deciduous forests on the Oregon Coast Range.

The Dunn's salamander is a lungless salamander, and it does not require moving water to breed (Nussbaum et al. 1983). It was significantly more abundant in riparian than upslope habitats in this study. The riparian influence was also evident with more captures at stream stations than stations further away from the stream. McComb et al. (1993) also captured more Dunn's salamanders along streamside than upslope transects. The species has been found more associated with aquatic habitats than other members of the *Plethodon* genus (Nussbaum et al. 1983, Bury 1988), and Blaustein et al. (1995) suggested that habitat disturbances that increase substrate temperatures and decrease moisture will be detrimental to Dunn's salamander populations. Our results support their conclusions and we suggest the maintenance of some mature coniferous forests in riparian areas would benefit the Dunn's salamander in managed areas on the Oregon Coast.

Nussbaum et al. (1983) suggested that the preferred habitat of the red-backed salamander is the dryer sections of dense coniferous forests. It was the only other member of the genus *Plethodon* captured in our study. Although it was found equally abundant between stream and upslope

habitats, it was captured in greater numbers in deciduous stands than other forest types. This is another species which might benefit from management that would include retention of some deciduous forests.

The Oregon salamander is a lungless salamander restricted to the coast of the Pacific Northwest and Coastal Northern California (Nussbaum et al. 1983). In this study, it was the only amphibian which was more abundant in the upslope than riparian habitats. Similarly, McComb et al. (1993) captured more Oregon salamanders in the upslope transects than streamside, and Welsh and Lind (1991) found abundances decreased as moisture increased in older forests. Nussbaum et al. (1983) suggested that Oregon salamanders usually preferred forested areas but have been found in clearings in the Pacific Northwest. Raphael (1984) found greater numbers of the Oregon salamanders in older Douglas-fir forests than in younger forest types in Northern California, and Bury (1983) found it more abundant in old-growth forests than in logged stands. The results from our study were similar to their findings; the Oregon salamander was less abundant in the shrub forest type especially in the upland areas.

Anurans

There are 6 families, 6 genera and 14 species of anurans which occur in the Pacific Northwest (Nussbaum et al. 1983). In contrast to the higher abundance of tailed frogs that we found in riparian versus upslope habitats, McComb et al. (1993) captured similar numbers of tailed frogs between stream and upslope transects in mature forests. It was found mostly in cooler sections of streams by Nussbaum et al. (1983) and Bury and Corn (1991). It requires permanent drainages often with a dense canopy cover for optimal temperatures (Noble and Putnam 1931, Nussbaum et al. 1983, Bury and Corn 1991). However, tailed frogs (especially the juveniles) have been found at long distances from permanent streams in forested areas (Corn and Bury 1990). Noble and Putnam (1931) found adult tailed frogs at greater distances away from the stream during the wet season and with higher abundances along the stream during dryer times. Noble and Putnam (1931) and Metter (1964) have suggested that habitat loss caused by logging and/or fire has resulted in the disappearance of tailed frogs. Our results support these. The tailed frog was more abundant in the large sawtimber and old-growth forests than the younger forest types. There were only three individuals captured in the shrub forest type and these were all within 25 m of the stream in this study. Bury (1968) suggested that the effect of timber removal on stream microclimate and tailed frog populations is dependent on the geography of the area. He found tailed frogs in recently logged locations of coastal Humboldt County, CA, where the maritime climate reduces the temperatures of the exposed stream bed. In contrast, we suggest that the maintenance of mature or old-growth coniferous forests will benefit the tailed frog in managed areas on the Oregon Coast.

The red-legged frog is restricted to the Pacific Northwest Coast and the coast of Northern California. Nussbaum et al. (1983) suggested that red-legged frogs may be found in riparian areas of moist forests in the Pacific Northwest. They are dependent on water for breeding; however, adults are semi-aquatic to terrestrial (Nussbaum et al. 1983), and individuals can be found up to 300 m away from standing water. Seventy-five percent of the red-legged frog captures in this study were along streams; however, two individuals were captured 200 m away in the upslope transect. Aubry and Hall (1991) found red-legged frogs more abundant in mature than young forests in the southern Washington Cascades. In contrast, the red-legged frog was most abundant in the deciduous forest type and was not found in the mature coniferous forests in this study. Bury and Corn (1991) suggested that red-legged frogs may prefer creeks and streams with low gradients for breeding and Nussbaum et al. (1983) suggested that breeding sites must have little or no flow. Results from our study suggest that red-legged frogs might be associated with some component of deciduous forests, although the relationship was weak possibly because of a small sample size. Alternatively, we suggest that populations of red-legged frogs might be more dependent on site-specific characteristics such as low stream flow and low abandance of predators, rather than vegetative type. Nussbaum et al. (1983) suggested that declining red-legged frog populations might be attributed, in part, to Bullfrog introductions and they suggested that roughskin newts may be important predators on eggs and larvae of red-legged frogs. Predators such as the Pacific giant salamanders and roughskin newts may have limited red-legged frog

populations in some areas in this study. Further investigation is necessary before conclusions may be made about this species.

Reptiles

The northern alligator lizard is an endemic species to the Pacific Northwest and Northern California and is the only lizard which occupies the coast of Northern Oregon and Washington (Nussbaum et al. 1983). In this study, the alligator lizard was more abundant in the shrub stands than in all other forest types and in the upslope versus stream transects. Similarly, Raphael (1984) found abundance of alligator lizards decreased with stand age in Douglas-fir forests in Northwestern California. Corn and Bury (1990) found few or no reptiles in young (>40 years), mature and old-growth forest sites in the Pacific Northwest and suggested that the closed canopy and lack of suitable open areas in these forests probably did not provide the necessary habitat requirements for this group. The lack of abundance of reptiles in forest types of our study, with the exception of the shrub forest type, supports their results. However, low snake captures in this study are probably a result of poor catch success for snakes using pitfall traps and the ability of snakes to escape from pitfall traps.

Riparian Associates

The tailed frog, Dunn's salamander and roughskin newt were significantly more abundant in riparian than upslope habitats and at distances closer to the stream than further away along the transriparian transects. These species may be considered riparian associates. In addition, the Pacific giant salamander and red-legged frog were captured more often along the stream transect than upslope and may depend on riparian habitat for at least part of their life requirements. In contrast, the Oregon salamander was significantly more abundant in the upslope than in the stream habitat.

These results suggest that small riparian systems provide important habitat for tailed frogs, Dunn's salamanders, roughskin newts, and Pacific giant salamanders in the Oregon Coast Ranges. There was a significant decline in captures of the first three species at 50-100 meters away from streams. Consequently, we suggest riparian management zones should be at least 75-100 m on each side of the stream to include features of riparian habitat and the areas of highest abundance of all of these species. Management for upslope/and or old forest associates (e.g., Oregon salamander and the Pacific giant salamander respectively) may be equally as important as for riparian species. It is vital that these systems be considered in management plans which include the protection of at least some of the areas from timber harvest. Many of these herpetofauna species have limited geographic ranges which includes only portions of the Pacific Northwest. Protection of these areas and species is critical. The tailed frog and red-legged frog are considered sensitive species in Oregon by Oregon Department of Fish and Wildlife. The importance of monitoring and maintaining populations of sensitive species is obvious.

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Status and Condition of Fish Assemblages in Streams of the Tualatin River Basin, Oregon

Abstract

We conducted fish inventories at 38 sites on fifteen streams of the lower Tualatin River Basin as part of a study to document fish species and assess the impacts of urbanization on native fish assemblages. We used three-pass electrofishing techniques to survey each site in spring, summer, autumn, and winter. We collected 25 species of fish from ten families; twelve species from five families (6.3% of the total catch) were exotic to Oregon. Reticulate sculpin *Cottus perplexus*, a native fish tolerant of habitat degradation, comprised 68.4% of the catch. Number of species per stream ranged from 5 to 15; number of native species ranged from 4 to 10. Sites in the upper sections of streams contained the largest number of trout, native minnows, and sculpins, whereas lower sites contained more diverse species assemblages and a larger number of introduced fish. We found a significant difference in the number of native species among sites of different stream order, but no significant difference when all species were considered. Our catch also varied seasonally, likely due to species motility, gear selection, and variation in life history stages. Native species intolerant to habitat disturbances (torrent sculpin *Cottus rhotheus* and *Oncorhynchus* spp.) comprised only 1.7% of the total catch, and 2.0% of the total catch exhibited parasites or physical anomalies. The relatively low number of intolerant species, high proportion of fish with parasites or anomalies at some sites, introduction of exotic species, and reported habitat deficiencies suggest that native fish assemblages in the basin are at least moderately unhealthy.

Introduction

Like many river systems near urban areas, the Tualatin River and its tributaries within the urban growth boundary near Portland, Oregon, have undergone substantial changes in water quality, fish habitat, and fish assemblages. Agricultural practices, sewage treatment plant discharges, water allocation, and urbanization are all factors that may contribute to diminished water quality. The hydrology of the Tualatin River Basin has changed significantly with logging practices and the urbanization of natural floodplains (Shively 1993). The Tualatin River Basin has been the subject of intensive water quality investigations in recent years (Wolf 1992; Ervin et al. 1993; Miner et al. 1993), and the U. S. Environmental Protection Agency sampled fish, benthos, and habitat at several sites in 1982 (R. M. Hughes, unpublished data). Results of fish assemblage surveys have not been previously published, and the long-term effects of habitat disturbances on fish may never be known.

Historic information regarding fish assemblages in the Tualatin River Basin is scarce. Past surveys focused primarily on salmonids, with other species usually referred to as "rough fish" or even "trash fish." A report by the Oregon State Game Commission in 1963 addressed the need to document species other than salmonids, and included some basic fish distribution data (Hutchison and Aney 1964). Dimick and Merryfield (1945) conducted extensive surveys of fishes of the Willamette River system, including some limited sampling of the Tualatin River and its tributaries. The Oregon Department of Fish and Wildlife (ODFW) has continued to perform occasional fish inventories, but information generally is limited to single day, non-replicated samples in the mainstem Tualatin River. In addition, consulting firms occasionally conduct site-specific fish surveys near construction or mitigation projects. Li and Gregory (1993) identified the need for a coordinated effort to survey all fish populations in the watershed.

The Tualatin River currently supports a significant warmwater fishery in its lower reaches, and limited opportunities for trout *Oncorhynchus* spp., including steelhead *O. mykiss*, in the upper reaches and tributaries. Once extensively stocked with hatchery trout, the basin now is being managed primarily for wild trout production. Approximately 60,000 coho salmon *O. kisutch* and 10,000 steelhead are planted annually as mitigation for the construction of a dam in the upper watershed (ODFW 1993).

This paper is part of a cooperative study by ODFW and the Unified Sewerage Agency of Washington County to evaluate the effects of urbanization on

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fish populations of the basin. Our objective is to document fish species and describe their relative abundance in streams of the Tualatin River Basin within the urban growth boundary near Portland, Oregon. We also examine species assemblages as possible indicators of degraded water quality and habitat. This information may help managers identify areas requiring protection because of the presence of native fish species intolerant of environmental degradation.

Study Area

The Tualatin River flows easterly from its headwaters in the Coast Range of northwestern Oregon to its confluence with the Willamette River at river kilometer 46.1 (Figure 1). Portions of all streams we studied flow through the urban growth boundary near Portland, Oregon. These streams are characterized by low gradient, heavy siltation, seasonal flooding, and temperature extremes, especially in the lower reaches (ODFW, unpublished data).

We identified 38 sites in the fifteen streams to be sampled (Figure 1; Table 1). Sites were 100 meters long and were selected based on accessibility and proximity to concurrent habitat surveys (Neill et al. 1995). We generally identified one site near the mouth of each stream and one site near the headwaters. In larger streams, we identified an additional site between the upper and lower sites. Sites are referred to by stream and relative location (lower, middle, or upper) throughout this paper.

Methods

We used electrofishing equipment to conduct three-pass-removal sampling of fish populations (Armour et al. 1983; Riley and Fausch 1992) in spring (April-May), summer (July-August), and autumn (October-November) 1994, and winter (January-February) 1995. The ends of each 100-meter site were blocked with nets to ensure population enclosure, except in autumn and winter, when we were unable to use block nets because of high stream flows. We sampled downstream to upstream using a model 12 Smith-Root backpack electrofisher. Voltage, pulse rate, and pulse width settings varied depending on water conductivity and fish recovery.

After each pass, specimens collected were counted, identified to species, and inspected for

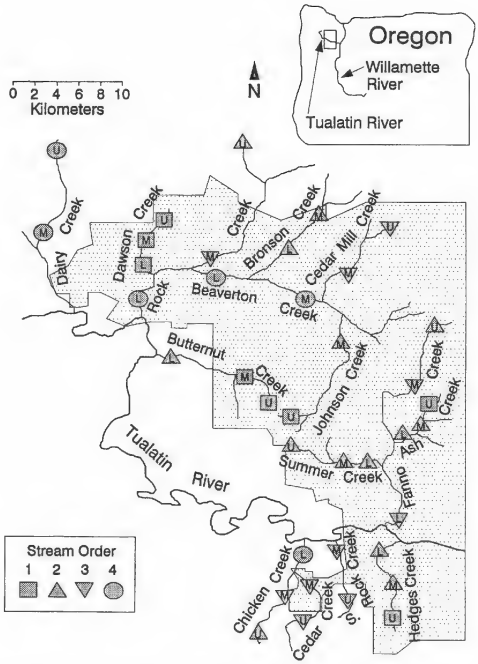

Figure 1. Streams of the Tualatin River Basin sampled in 1994-95. Stream order determined by methods described by Strahler (1957); minor tributaries not shown. Shaded area approximates urban growth boundary of Washington County, Oregon. L = Lower, M = Middle, U = Upper.

parasites or physical anomalies. We measured (fork length to nearest millimeter) up to 100 individuals of each species. To reduce mortality, we returned all fish to the stream below the downstream end of the site prior to the next pass.

We determined origin (native or introduced) and relative tolerance of organic pollution, warm water, and sedimentation (Hughes and Gammon 1987) for each species collected. For species not described by Hughes and Gammon, we determined tolerance assignments from species descriptions in Scott and Crossman (1973), Moyle (1976), and Wydoski and Whitney (1979).

We summarized our catch by species and family and constructed a site-species matrix to compare the relative occurrence of species among different streams, sites within streams, and stream orders. The number of species usually increases with increasing stream order in undisturbed waters (Lotrich 1973; Kuehne 1962; Moyle and Cech

TABLE 1. Streams of the Tualatin River Basin surveyed in 1994-95. L = Lower, M = Middle, U = Upper.

Creek	Mainstem length (km)	Number of sites (Location)	Sites sampled by season			
			Spring	Summer	Autumn	Winter
Hedges	3.8	3 (L,M,U)	3	2	2	2
Fanno	21.7	3 (L,M,U)	3	3	3	2
Ash	5.7	3 (L,M,U)	3	3	3	3
Summer	5.2	3 (L,M,U)	3	3	2	3
South Rock	8.4	2 (M,U)	2	2	2	0
Chicken	9.7	3 (L,M,U)	3	3	3	2
Cedar	10.9	2 (M,U)	2	2	2	1
Butternut	8.4	3 (L,M,U)	3	3	3	2
Rock	28.7	3 (L,M,U)	3	2	1	1
Dawson	6.5	3 (L,M,U)	3	2	1	1
Beaverton	15.3	2 (L,M)	2	2	1	0
Bronson	10.7	2 (L,M)	2	2	2	2
Cedar Mill	9.5	2 (M,U)	2	2	2	2
Johnson	6.3	2 (M,U)	2	1	1	1
Dairy	42.2	2 (M,U)	2	2	1	0

1988). To assess the degree of disturbance in the Tualatin River Basin, we used the Kruskal-Wallis test (Sokal and Rohlf 1981) to compare the mean number of species present among stream orders.

We examined seasonal trends in the relative abundance of various species, and constructed length-frequency histograms for eight commonly observed species to determine whether recruitment affected seasonal variation in the number of these species. We also described the general distributions of intolerant and introduced species. We determined the percent of fish exhibiting parasites or anomalies as a possible indicator of habitat or water quality problems.

Results

We collected 42,219 fish from ten families and sixteen genera in streams of the Tualatin River Basin (Table 2). Reticulate sculpin was the most abundant species; redside shiner, threespine stickleback, speckled dace, and mosquitofish also were common. Twelve fish species from five families were introduced and comprised 6.3% of the total catch.

Species intolerant of warm water, sedimentation, and organic pollution comprised 1.7% of the total catch and included torrent sculpin, cutthroat trout, rainbow trout, and coho salmon. Torrent sculpin were found only in upper Dairy Creek (Figure 1), a free-flowing, forested site free from obvious urban or agricultural influences. The majority (80.7%) of cutthroat and rainbow trout also were captured at this site. Coho salmon were observed only in lower Fanno Creek.

Fish assemblages varied widely among streams and among sites within streams (Table 3). Total number of species per stream ranged from 5 in Johnson Creek to 15 in Summer Creek, whereas the number of native species ranged from 4 (Hedges and Johnson creeks) to 10 (Fanno, Chicken, and Rock creeks). Among specific sites, upper Butternut Creek contained the fewest species (1); lower Fanno and middle Summer creeks contained the most (13). The number of native species ranged from zero in upper Summer Creek to nine in lower Fanno, middle South Rock, and middle Chicken creeks. In general, sites in the upper sections of streams contained the largest numbers of trout, native minnows, and sculpins, whereas lower sites contained more diverse species assemblages and a larger number of introduced fish. Most sunfish (80.9%) and many mosquitofish (44.7%) were captured at three second-order sites (middle Hedges, middle Summer, and upper Summer creeks) near large ponds or wetlands. Three upper sites that were free-flowing, forested, and appeared free of major urban or agricultural influences (upper Dairy, upper Chicken, and upper Rock creeks) contained primarily trout and sculpin species.

TABLE 2. Fish collected in streams of the Tualatin River Basin, 1994-95. A small percentage (0.59) of the catch was not identified to species; introduced species comprised 6.3% of the total catch. Relative tolerance refers to physiological resistance to organic pollution, warm water, and sedimentation (Hughes and Gammon 1987; Scott and Crossman 1973; Moyle 1976; Wydoski and Whitney 1979).

Family, Species	Percent of catch	Relative tolerance
Petromyzontidae		
Western brook lamprey *Lampetra richardsoni*	0.64	Intermediate
Pacific lamprey *Lampetra tridentata*	0.73	Intermediate
Salmonidae		
Coho salmon *Oncorhynchus kisutch*	0.02	Intolerant
Cutthroat trout *Oncorhynchus clarki*	1.26	Intolerant
Rainbow trout *Oncorhynchus mykiss*	0.23	Intolerant
Cyprinidae		
Redside shiner *Richardsonius balteatus*	7.38	Intermediate
Speckled dace *Rhinichthys osculus*	4.82	Intermediate
Northern squawfish *Ptychochelius oregonensis*	0.01	Tolerant
Fathead minnow *Pimephales promelas*[a]	0.07	Tolerant
Goldfish *Carassius auratus*[a]	0.07	Tolerant
Catostomidae		
Largescale sucker *Catostomus macrocheilus*	1.41	Tolerant
Ictaluridae[b]		
Yellow bullhead *Ameiurus natalis*	0.22	Tolerant
Brown bullhead *Ameiurus nebulosus*	0.01	Tolerant
Poeciliidae[b]		
Mosquitofish *Gambusia affinis*	3.09	Tolerant
Gasterosteidae		
Threespine stickleback *Gasterosteus aculeatus*	7.14	Intermediate
Centrarchidae[b]		
Largemouth bass *Micropterus salmoides*	0.38	Tolerant
Bluegill *Lepomis macrochirus*	0.81	Tolerant
Pumpkinseed *Lepomis gibbosus*	1.40	Tolerant
Warmouth *Lepomis gulosus*	0.02	Tolerant
Black crappie *Pomoxis nigromaculatus*	0.01	Tolerant
White crappie *Pomoxis annularis*	<0.01	Tolerant
Percidae[b]		
Yellow perch *Perca flavescens*	0.03	Intermediate
Cottidae		
Reticulate sculpin *Cottus perplexus*	68.40	Tolerant
Prickly sculpin *Cottus asper*	1.12	Intermediate
Torrent sculpin *Cottus rhotheus*	0.19	Intolerant

[a]Introduced species.

[b]Introduced family.

Species assemblages also varied considerably among stream orders (Table 3; Figure 2). First-order stream sites contained a large proportion of sculpins, native minnows, and threespine stickleback. The proportion of sculpins increased with increasing stream order, whereas the proportion of minnows and threespine stickleback decreased. Sculpins dominated the catch in third and fourth-order stream sites, and trout were captured primarily in fourth-order stream sites. Introduced fish comprised 14.7% of the catch in second-order sites, but only 2.3% in other sites.

The average number of fish species captured per site generally increased with increasing stream order (Figure 3). For all species combined, we observed the greatest increase in species diversity from first to second-order sites, largely because of the high occurrence of introduced fish in several second-order sites. The mean number of native fishes increased more uniformly with stream order. Kruskal-Wallis tests indicated a significant ($P = 0.02$) difference in the number of native species among stream orders; however, we found no significant difference among stream orders ($P = 0.12$) for all species combined.

TABLE 3. Presence/absence matrix by stream order for fish collected in tributaries of the Tualatin River, 1994–95. L = Lower site, M = Middle site, U = Upper site. Relative occurrence: R = Rare, comprised <2% of catch, I = Intermediate, comprised 2–20% of catch, C = Common, comprised >20% of catch, – = not present.

	Species																								
Order, Site	Brook Lamprey	Pacific Lamprey	Coho Salmon	Cutthroat Trout	Rainbow Trout	Redside Shiner	Speckled Dace	Northern Squawfish	Fathead Minnow	Goldfish	Largescale Sucker	Yellow Bullhead	Brown Bullhead	Mosquitofish	Threespine Stickleback	Largemouth Bass	Bluegill	Pumpkinseed	Warmouth	Black Crappie	White Crappie	Yellow Perch	Reticulate Sculpin	Prickly Sculpin	Torrent Sculpin
First Order																									
Hedges U	I	C	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	I	–	–
Ash U	–	–	–	–	–	I	R	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	C	–	–
Butternut M	–	–	–	–	–	–	C	–	–	–	–	–	–	R	C	–	–	–	–	–	–	–	C	–	–
Butternut U	–	–	–	–	–	–	C	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Dawson L	R	R	–	R	–	R	I	–	–	–	R	–	R	R	I	–	R	–	–	–	–	–	C	–	–
Dawson M	R	R	–	–	–	R	C	–	–	–	–	–	–	–	C	–	–	–	–	–	–	–	C	–	–
Dawson U	–	–	–	–	–	I	C	–	–	–	–	–	–	–	C	–	R	–	–	–	–	–	C	–	–
Johnson U	–	–	–	–	–	–	I	–	–	–	–	–	–	C	–	–	–	–	–	–	–	–	–	–	–
Second Order																									
Hedges L	–	–	–	–	–	–	–	–	–	–	–	–	–	R	I	–	–	–	–	–	–	–	C	–	–
Hedges M	–	–	–	–	–	–	–	–	–	–	–	–	R	C	R	I	I	C	–	–	–	–	I	–	–
Fanno U	R	R	–	R	–	I	I	–	–	–	–	–	–	R	–	–	–	–	–	–	–	–	C	–	–
Ash L	–	–	–	–	–	I	R	–	–	R	I	–	–	I	I	R	R	R	–	–	–	–	C	–	–
Ash M	–	–	–	–	–	C	R	–	–	–	R	–	–	–	–	–	–	–	–	–	–	–	C	–	–
Summer L	R	I	–	–	–	I	R	–	–	–	I	R	–	R	–	R	R	I	–	–	–	–	C	–	–
Summer M	R	R	–	–	–	C	–	–	–	R	R	I	–	I	R	I	I	I	–	–	–	R	I	–	–
Summer U	–	–	–	–	–	–	–	–	R	–	–	R	–	C	–	I	C	C	–	–	–	R	–	–	–
Chicken U	–	R	–	I	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	C	–	–
Butternut L	R	R	–	R	–	–	–	–	–	–	R	–	–	R	R	–	R	–	R	–	–	–	C	–	–
Rock U	–	–	–	I	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	C	–	–
Bronson M	I	R	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	C	–	–
Bronson U	I	I	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	C	–	–
Johnson M	–	–	–	–	–	I	R	–	–	–	–	–	–	C	C	–	–	–	–	–	–	–	I	–	–

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	Brook Lamprey	Pacific Lamprey	Coho Salmon	Cutthroat Trout	Rainbow Trout	Redside Shiner	Speckled Dace	Northern Squawfish	Fathead Minnow	Goldfish	Largescale Sucker	Yellow Bullhead	Brown Bullhead	Mosquitofish	Threespine Stickleback	Largemouth Bass	Bluegill	Pumpkinseed	Warmouth	Black Crappie	White Crappie	Yellow Perch	Reticulate Sculpin	Prickly Sculpin	Torrent Sculpin
Third Order																									
Fanno L	R	R	R	R	–	–	R	–	–	–	R	–	–	–	–	–	–	R	–	–	–	–	C	I	–
Fanno M	R	R	–	R	–	C	R	–	–	–	R	–	–	–	–	–	–	–	–	–	–	–	C	–	–
S. Rock M	R	R	–	R	–	R	R	–	–	–	R	–	–	R	I	–	–	–	–	R	–	–	C	I	–
S. Rock U	–	–	–	R	–	–	–	–	–	–	–	–	–	I	C	–	–	–	–	–	–	–	C	R	–
Chicken M	I	R	–	R	–	I	R	–	–	–	R	–	–	–	R	–	–	–	–	–	–	–	C	R	–
Cedar M	–	R	–	–	–	I	–	–	–	–	R	–	–	–	C	R	–	–	–	–	–	–	C	–	–
Cedar U	I	I	–	R	–	I	–	–	–	–	I	–	–	–	I	–	–	–	–	–	–	–	C	–	–
Rock M	R	–	–	R	–	I	–	–	–	–	I	–	R	R	C	R	–	–	R	–	–	–	C	–	–
Bronson L	–	R	–	–	–	–	R	–	–	–	–	–	–	I	C	R	–	–	–	–	–	–	C	R	–
Cedar Mill M	R	–	–	R	–	–	–	–	–	–	R	R	–	R	I	–	–	–	R	R	–	–	C	–	–
Johnson U	R	I	–	–	–	–	–	–	R	–	–	–	–	–	–	–	I	–	–	–	–	–	C	–	I
Fourth Order																									
Chicken L	I	I	–	–	R	I	R	–	–	–	R	–	R	I	C	–	–	–	–	–	–	–	C	I	–
Rock L	R	R	–	–	R	R	R	R	–	–	R	–	–	R	C	–	–	–	–	–	–	–	C	–	–
Beaverton L	–	R	–	–	–	–	R	–	–	–	R	–	–	R	I	–	–	–	–	–	–	–	C	–	–
Beaverton M	R	R	–	R	–	I	R	–	–	–	R	–	R	I	I	R	–	–	–	–	–	–	C	–	–
Dairy M	–	R	–	R	–	I	–	–	–	–	I	–	–	–	–	–	–	–	R	–	–	–	C	–	–
Dairy U	R	R	–	C	I	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	C	–	I

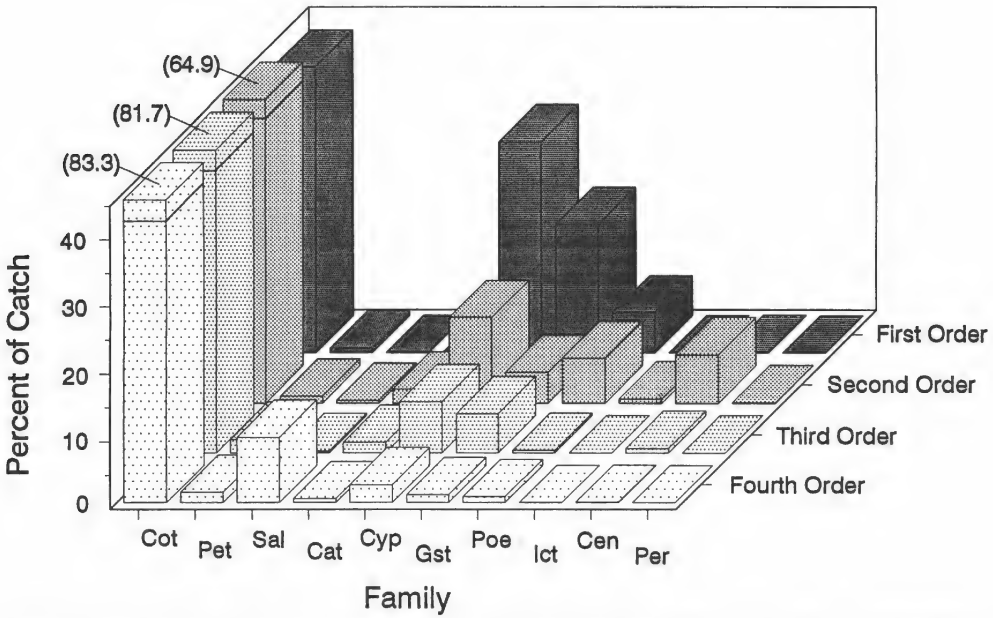

Figure 2. Percent of catch by family and stream order in the Tualatin River Basin, 1994-95. Pet = Petromyzontidae, Sal = Salmonidae, Cat = Catostomidae, Cyp = Cyprinidae, Gst = Gasterosteidae, Poe = Poeciliidae, Ict = Ictaluridae, Cen = Centrarchidae, Per = Percidae, and Cot = Cottidae.

Fish assemblages also varied seasonally (Figure 4). The proportion of minnows in our catch increased considerably from spring to winter, and the proportion of sculpins decreased over the same period. We captured the highest proportion of trout during summer sampling, whereas largescale sucker, threespine stickleback, and mosquitofish were common during autumn sampling.

Length-frequency histograms (Figure 5) for the eight most commonly observed species (reticulate sculpin, redside shiner, threespine stickleback, speckled dace, mosquitofish, largescale sucker, pumpkinseed, and cutthroat trout) were highly variable. Histograms for mosquitofish, threespine stickleback, and cutthroat trout showed relatively high numbers of small fish in certain seasons: winter and spring for mosquitofish, summer for trout, and spring for threespine stickleback.

We found parasites or physical anomalies on 2.0% of all fish captured. Parasites generally were leeches (Class Hirudinea) or worms (Class Nematoda); a small proportion of fish had fungal infections, lesions, or physical deformities. The percent of fish with parasites or anomalies was highest for redside shiner (8.4), largescale sucker (5.1), and cutthroat trout (3.6), and ranged from 0.0 to 15.1 among stream sites. Parasites or anomalies were present on more than 5% of the catch in five of 38 sites surveyed (middle Fanno, lower Summer, middle Summer, lower Dawson, and middle Cedar Mill creeks).

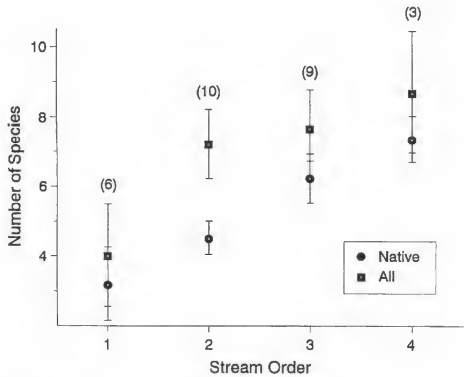

Figure 3. Mean number (and 95% confidence intervals) of species collected per site for each stream order in the Tualatin River Basin, 1994-95.

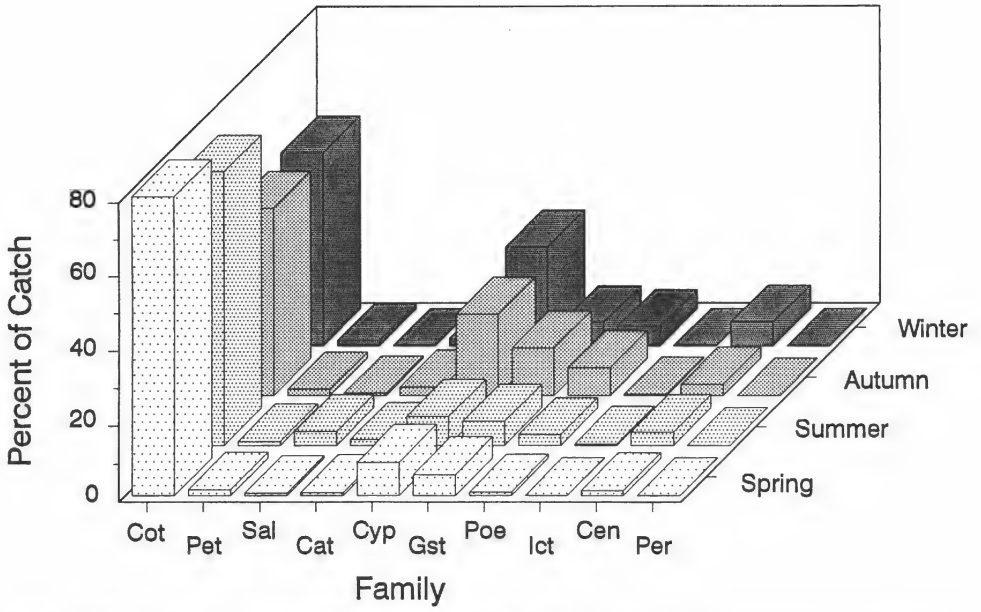

Figure 4. Percent of catch by family and season in the Tualatin River Basin, 1994-95. Pet = Petromyzontidae, Sal = Salmonidae, Cat = Catostomidae, Cyp = Cyprinidae, Gst = Gasterosteidae, Poe = Poeciliidae, Ict = Ictaluridae, Cen = Centrarchidae, Per = Percidae, and Cot = Cottidae.

Discussion

The results of our surveys may be broadly compared to previous surveys in the Willamette River near the Tualatin River (Hughes and Gammon 1987; Farr and Ward 1993). Farr and Ward (1993) reported 39 fish species from 17 families in the lower Willamette River (downstream from river kilometer 27). Nineteen of these species were absent from our catch in the Tualatin River Basin. Hughes and Gammon (1987) surveyed the Willamette River up to river kilometer 283, including two sampling sites near the mouth of the Tualatin River. Eight species not observed in our survey of the Tualatin River Basin were captured at these sites. Species common to both Willamette River surveys, but not represented in our catch included mountain whitefish *Prosopium williamsoni*, mountain sucker *Catostomus platyrhynchus*, chinook salmon *Oncorhynchus tshawytscha*, chiselmouth *Acrochelius alutaceus*, peamouth *Mylocheilus caurinus*, common carp *Cyprinus carpio*, and smallmouth bass *Micropterus dolomieui*. We captured three species (brook lamprey, fathead minnow, and mosquitofish) not described by Farr and Ward (1993) or Hughes and Gammon (1987).

The smaller number of species occurring in the Tualatin River Basin may be attributable to a variety of factors. Willamette Falls, at Rkm 43.0 of the Willamette River, is a barrier to fish passage and may exclude species such as starry flounder *Platichthys stellatus* and American shad *Alosa sapidissima* from the Tualatin River. Chinook salmon probably were never abundant in the Tualatin River Basin (ODFW 1993). Mountain whitefish, peamouth, mountain sucker, and chiselmouth may be unable to survive in Tualatin River tributaries due to predation by introduced species, interspecific competition, poor water quality, or other habitat perturbations. These species may also prefer larger streams, as evidenced by their presence in the mainstem Willamette River. Common carp and smallmouth bass have been observed at other locations within the Tualatin River Basin (ODFW, unpublished data).

Dimick and Merryfield (1945) reported nine native species from five families and two introduced species from two families in the mainstem Tualatin River and one tributary (Scroggin Creek, since renamed Scoggins Creek). They identified two species, chislemouth and riffle sculpin *Cottus*

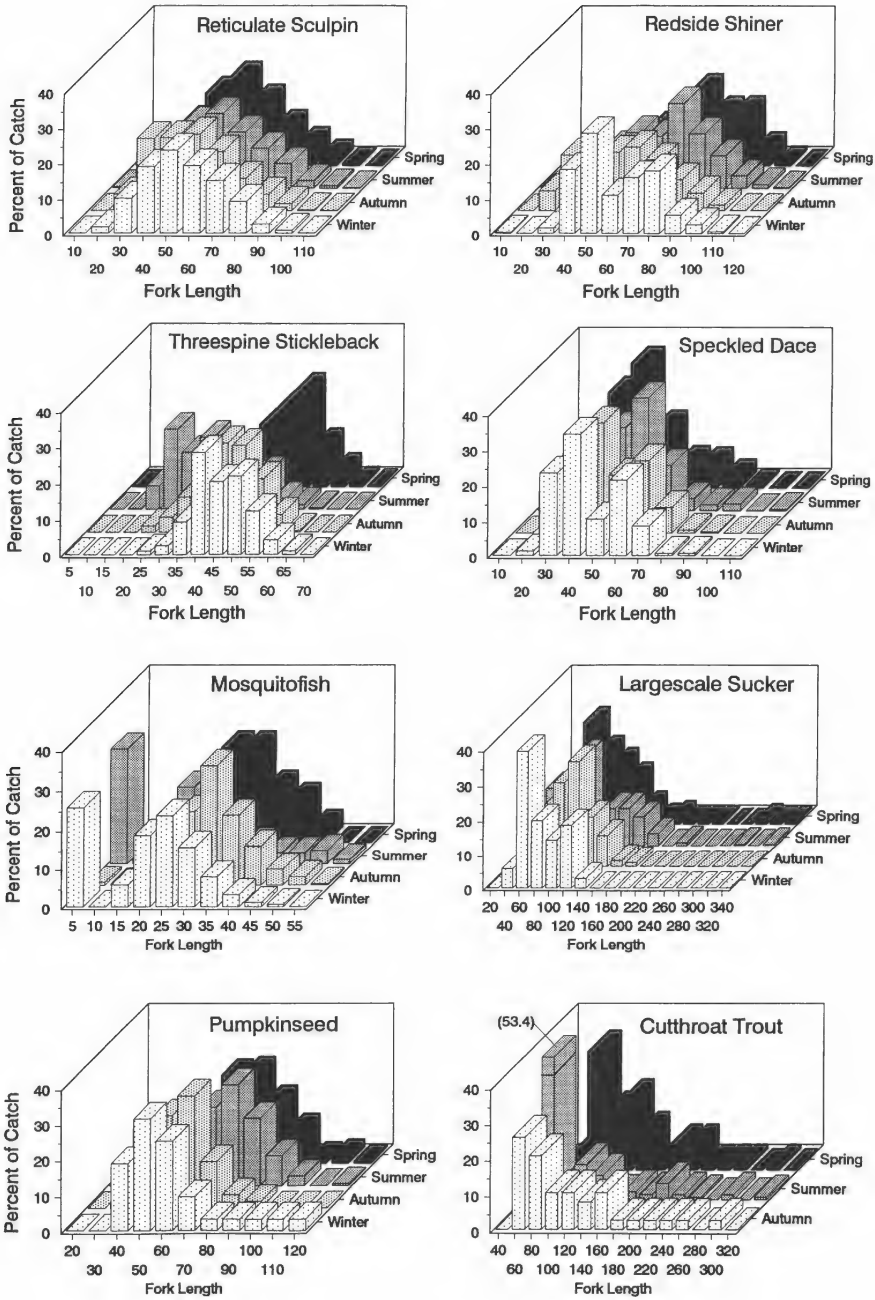

Figure 5. Length-frequency histograms for eight species comprising the greatest proportion of the catch in the Tualatin River Basin, 1994-95. Winter length-frequency data for cutthroat trout is omitted due to a very small sample size (N = 3).

gulosus, not observed in our surveys. However, it is believed that early literature did not recognize taxonomic distinctions between riffle sculpin and reticulate sculpin (Wydoski and Whitney 1979); therefore, Dimick and Merryfield (1945) most likely described reticulate sculpin considering the large number of this species we collected in tributaries of the Tualatin River. Although we identified fourteen more native species and eight more introduced species than Dimick and Merryfield (1945), a direct comparison to their work is probably inappropriate, as we surveyed a greater number of sites, none in the mainstem Tualatin River. However, we can say that ten of the eleven species recorded by Dimick and Merryfield in the 1940's also were present in the current study.

Introduced species appear to be well established at certain sites within the Tualatin River Basin. One such species, the fathead minnow, does not appear in any historical surveys of the Tualatin or Willamette rivers, and may be a recent introduction. The large number of sunfish and mosquitofish found near wetland areas reflects the ability of these species to proliferate in warm, shallow, weedy water, and should be a consideration for future mitigation projects specifying the construction of wetlands.

Intolerant species were relatively uncommon, but occurred in large numbers at the three sites that were forested, free-flowing, and apparently unaffected by urban or agricultural influences. However, trout or salmon were observed in smaller numbers at sixteen additional sites. No adult salmon or steelhead were observed, although it is likely that the rainbow trout captured were juvenile steelhead (Jay Massey, ODFW, personal communication).

Species diversity in temperate streams usually increases with increasing stream order (Kuehne 1962; Lotrich 1973). However, in systems affected by flooding, water removal by humans, or pollution, the number of species may decrease in larger order streams (Moyle and Cech 1988). The number of native species increased significantly with increasing stream order in the Tualatin River Basin; however, the number of all species did not differ significantly among stream orders, suggesting possible disturbances. Because the historic composition of fish assemblages in the basin is largely unknown, the effect of species addition or replacement on the relationship between number of species and stream order remains uncertain.

The variability of species assemblages among seasons may be due to a variety of factors. Highly mobile species such as cutthroat trout may move throughout the basin to spawn or avoid high flows and temperature. The relatively high percentage of trout captured in upper Dairy Creek during summer sampling supports this point. Gear selectivity probably also plays a role in the observed seasonal patterns. Benthic species such as sculpin were often more difficult to capture at high flows or in turbid water, causing a decrease in the proportion of these species and an apparent increase in the proportion of more catchable pelagic species (i.e. Cyprinids) collected in autumn and winter.

Differences in catch among seasons may also be partially due to variability in the size structure of certain species. Although we routinely captured fish as small as 5 mm, our gear was not able to sample larval stages of most species. However, length-frequency histograms (Figure 5) indicate that we sampled early life stages for at least some species. The greatest proportion of small cutthroat trout and threespine stickleback, for example, were captured during or immediately after the known spawning periods for these species (spring and early summer, respectively; Wydoski and Whitney 1979). Although mosquitofish may spawn during all seasons (Moyle 1976), we observed large abundances of small fish in spring and winter.

Although not generally the cause of major fish kills, parasites may render fish susceptible to secondary infections or weaken their tolerance of environmental changes (Herman 1990). The relatively high incidence (>5%; Karr et al. 1986) of parasites and anomalies in fish at several sites in our study area may be indicative of poor water quality or other habitat disturbances. The relatively high proportion of parasites or anomalies observed in cutthroat trout, an intolerant species, is also cause for concern.

The status of fish habitat in our study area undoubtedly impacts fish populations to some degree. Neill et al. (1995) report that many sites in this study area have habitat characteristics that do not meet those required by native fish species. Siltation, bank erosion, lack of woody debris, and insufficient overhead cover (presumably resulting in increased water

temperatures) are factors significantly affecting fish habitat at these sites.

The occurrence of introduced species and parasitic infestations, the low number of intolerant species, and poor habitat quality indicate that native fish assemblages in the Tualatin River Basin within the urban growth boundary near Portland, Oregon are at least moderately unhealthy. A number of sites contain few or no native species or a large number of fish affected by parasites or physical anomalies. Because some sites are able to support populations of cutthroat trout and other intolerant species, they are likely important seasonal refuges and may contain critical spawning and rearing habitat. Fish habitat in these streams should be preserved or enhanced whenever possible to ensure the continued success of these species, and of all fauna dependent on the basin. Although further changes in the basin probably are unavoidable due to continued urban growth, the health of watersheds such as the Tualatin River Basin are considered by many as important to the overall quality of life.

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Spatial Patterns of Tree Mortality in an Old-Growth *Abies–Pseudotsuga* Stand

Abstract

The processes that generate spatial patterns of organisms are often inferred from analysis of the patterns themselves. To test the reliability of such inferences, we examined spatial patterns of tree mortality over 16 years in a permanent 1-ha study area where causes of mortality are reasonably well known. The area is an old-growth stand in the Cascade Mountains of Oregon, dominated by *Abies amabilis* (60% of stems but only 12% of basal area), *Abies procera* (52% of basal area), and *Pseudotsuga menziesii* (22% of basal area). Mortality was dominated by the two *Abies* species. Dying *A. amabilis* occupied lower canopy strata and often had been suppressed or damaged by falling limbs or trees. Dying *A. procera* occupied upper canopy strata and often had been attacked by pathogens. The positions of dying trees and causes of mortality suggested that dying *A. amabilis* should be found near canopy trees and that dying *A. procera* should be aggregated. These hypotheses were tested by quadrat- and distance-based methods. On average, dying *A. amabilis* were not significantly closer to canopy trees than expected for a random distribution or closer than random selections of trees from the entire population of *A. amabilis*. Dying *A. procera* were aggregated at a scale of about 20 m; however, the degree of aggregation was not significant compared with the distribution of the entire population. The potential for large falling trees to strike other trees at some distance from their bases, and the underlying non-random distribution of some tree populations, may limit the extent to which causes of tree mortality can be inferred from spatial patterns.

Introduction

Understanding the causes of spatial patterns of organisms is a primary goal of ecology (Greig-Smith 1983, Ludwig and Reynolds 1988). Often, spatial patterns are analyzed to determine which processes generated the patterns. However, the degree to which pattern can be used to infer process is an open question, one requiring critical examination (Cale et al. 1989). One means of testing the proposition that pattern can be used to deduce process is to examine patterns generated by known processes. In this paper we examine spatial patterns of tree mortality in a permanent study area where the causes of mortality are reasonably well known.

The study area, a 1-ha portion of the H. J. Andrews Experimental Forest in western Oregon, provides an appropriate setting in which to test whether spatial patterns of tree mortality concur with predictions based on underlying processes. As described below (see Results), the two species accounting for most of the tree mortality, *Abies amabilis* (Pacific silver fir) and *A. procera* (noble fir), have contrasting causes of mortality, and dying trees occupy different canopy positions. Damage from falling green trees or limbs and suppression are the predominant causes of *A. amabilis* mortality; nearly all dying trees occupy lower canopy strata. *A. procera* mortality is often caused by pathogens; most dying trees occupy upper canopy strata.

Because of these differences in mortality patterns, one would expect different spatial patterns for the two tree species. Falling trees often strike and kill other trees in mature and old-growth forest stands in the Pacific Northwest (Franklin et al. 1987). In multicohort or uneven-aged stands such as our study area, shading and suppression also lead to mortality of younger, smaller trees (Oliver and Larson 1990). Thus, small trees near canopy trees should be most likely to die. Large trees, on the other hand, are more likely to succumb to pathogens or wind (Franklin et al. 1987). Pathogens, in particular, may affect groups of trees within stands, especially when dispersal of the pathogens is limited (*e.g.,* the root rot *Armillaria mellea*, which spreads through the soil (Manion 1981)). We therefore used the spatial data collected in the study area to test separate hypotheses for the two species:

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1) Dying *Abies amabilis* trees are near canopy trees observed when the study began;
2) Dying *Abies procera* trees are aggregated.

Study Area

The study area is in an old-growth forest in the *Abies amabilis* zone (Dyrness et al. 1974), in the H. J. Andrews Experimental Forest near Blue River, Oregon (44° 16' N lat., 112° 8' W long.). The elevation is 1290 m, with a south-facing slope of 5 percent. Soils on the study area belong to the Haplumbrept great group and are moderately deep and stony; they developed in andesitic glacial till mixed with volcanic ash and pumice (C. T. Dyrness, pers. comm.).

The canopy is predominately of *A. procera* and *Pseudotsuga menziesii* (Douglas-fir). Other canopy species include *Abies amabilis*, *Tsuga heterophylla* (western hemlock), and *T. mertensiana* (mountain hemlock). The understory is dominated by *Xerophyllum tenax* (beargrass).

Methods

Field methods

The study area was established as a 1-ha square in 1977 by researchers from the Pacific Northwest Research Station and Oregon State University (Franklin and Van Pelt 1990). All trees ≥ 5 cm dbh were tagged and mapped in relation to a grid of string placed at 5-m intervals. Accuracy of this method of tree mapping is estimated to be ± 1 m (Hawk et al. 1978). Trees were remeasured in 1983, 1988, and 1993. The area was surveyed annually from 1978 to 1991 for tree mortality. During the 5-year remeasurements and annual surveys, conditions of newly dead trees and any obvious causes of mortality were recorded.

Analytical methods

To provide necessary background for tests of spatial hypotheses, we summarized stand structure and mortality by species. In preliminary analyses, we noted that a very few *A. amabilis* were also canopy trees. Because we were interested in the relationship between the canopy and the smaller *A. amabilis* trees, we excluded *A. amabilis* canopy trees from the *A. amabilis* population in the spatial analyses.

To test hypotheses, we used quadrat-based and distance-based methods. Quadrat-based methods included 2 x 2 contingency tables (Sokal and Rohlf 1981; Greig-Smith 1983) and Morisita's index, I_d (Pielou 1977; Krebs 1989). Quadrat sizes ranging from 1 x 1 m to 20 x 20 m were used to test for pattern at a variety of spatial scales. The 2 x 2 contingency table method tests whether two populations (*i.e.*, dying *A. amabilis* and canopy trees) co-occur more or less often than would be expected from their respective densities (Greig-Smith 1983). Morisita's index, used to test aggregation of dying *A. procera*, is based on comparison of the probability that any two individuals drawn at random from the observed population will be from the same quadrat and the corresponding probability for a population with a random spatial pattern (Pielou 1977). Values of I_d greater than 1 indicate some degree of clumping; values less than 1 indicate a more regular distribution.

The quadrat-based statistical tests of spatial pattern compare observed patterns of dying trees with expectations under random distribution. The tests do not take into account the spatial patterns of all individuals of a species. However, if the underlying pattern of all individuals is ignored, it is possible to mistake patterns of dying trees for patterns intrinsic to a species. Therefore, in addition to testing patterns of dying trees relative to random distributions, we also performed randomization tests using the respective species' entire populations (Crowley 1992). For these tests, we repeatedly drew a random sample from the species' population equal in size to the number observed dying. For each random sample, the spatial statistic was computed and compared with the observed value of the statistic. The reported values of P are the fraction of times a value of the statistic at least as extreme as the observed value occurred in 1000 random samplings (Crowley 1992).

Distance-based methods included both univariate and bivariate combined count–distance statistics (Ripley's K(t) function, Mouer 1993; see also Kenkel 1988). Ripley's K(t) takes into account the location of all individuals, not just nearest neighbors, to describe spatial patterns (Kenkel 1988). K(t) is essentially a summation of all individuals within distance t of a target individual, averaged over all target individuals. Because some of the near neighbors of target individuals close to plot boundaries may lie outside of the plot, a correction is employed for edge effects (Mouer 1993). The correction imposes a weighting that

is the inverse of the proportion within the plot of the circumference of a circle centered on the target tree and passing through the near neighbor. With the correction factor,

$$K(t) = A * \sum_{i=1}^{n} \sum_{i=1}^{n} w_{ij}(t)/n^2 \quad \text{for } i \neq j$$

for all pairs of trees with $t_{ij} \leq t$,

where $K(t)$ = Ripley's K for distance t,
A = area of the plot,
n = the number of trees
$w_{ij}(t)$ = edge-correction weighting factor, and
t_{ij} = distance between trees i and j (Mouer 1993).

To assess spatial patterns at a range of scales comparable to those in the quadrat-based analyses, the combined count-distance statistics were computed for distances from 1 to 30 m.

To convert to a scale more convenient for assessing spatial pattern at a range of spatial scales, K(t) is transformed as follows:

$L(t) = t - (K(t) / \pi)^{1/2}$ (Kenkel 1988).

L(t) has an expectation of zero for random patterns; values greater than zero indicate more regular patterns, and values less than zero indicate more aggregated patterns (Kenkel 1988). K12(t) is a bivariate analog of K(t) that allows assessment of attraction or repulsion between two species or other classes of trees (Kenkel 1988; Mouer 1993). The analogous transformation of K12(t) to L12(t) is used to facilitate examination of patterns at a range of spatial scales. Positive values of L12(t) indicate repulsion between types; negative values indicate attraction.

Observed values of L(t) and L12(t) are compared with results from randomly generated sets of points to determine significance. Following Mouer (1993), we computed the statistics for 200 randomly drawn sets of points and generated one-sided 95 percent confidence envelopes. Since this technique does not take into account the spatial patterns of all individuals of a species, we also constructed "random mortality" confidence envelopes (see Kenkel 1988) by drawing 200 random samples from the initial populations of the species. The observed values of L(t) and L12(t) were compared with both the random and the random mortality 95 percent confidence envelopes.

Results

Stand structure

Abies amabilis accounted for 60 percent (393 stems) of the 651 stems in the 1-ha plot (Table 1). However, the total basal area of 86.8 m^2/ha was dominated by *A. procera* (52% of total), and to a lesser extent, *P. menziesii* (22%) (Table 2). The size distribution of *A. amabilis* contrasted with that of the species dominating the canopy (Fig. 1). *Abies amabilis* had a reverse-J-shaped size distribution, with an overwhelming majority of small stems, whereas both *A. procera* and *P. menziesii* had very few small stems and large median stem sizes (82 and 88 cm, respectively).

TABLE 1. Decrease in number of stems due to tree mortality, by species, 1977–1993.

Species	Number in original population (1977)	Number dying, 1977-1993	% original population dying	% dying per annum[1]
Abies amabilis	393	40	10.2	0.7
Abies procera	82	38	46.3	3.8
Pseudotsuga menziesii	30	0	0	0
Tsuga heterophylla	83	5	6.0	0.4
Tsuga mertensiana	63	7	11.1	0.7
All species	651	90	13.8	0.9

[1]Computed by the negative compound interest formula (Lorimer 1981) from percentage of original population dying.

TABLE 2. Decrease in basal area (m^2/ha) due to tree mortality by species, 1977-1993.

Species	Basal area in original population (1977)	Basal area lost to mortality, 1977-1993	% original basal area lost	% per annum[1]
Abies amabilis	10.2	2.7	26.2	1.9
Abies procera	45.0	18.7	41.5	3.3
Pseudotsuga menziesii	19.0	0	0	0
Tsuga heterophylla	5.6	0.02	0.4	0.03
Tsuga mertensiana	7.0	0.7	9.5	0.6
All species	86.8	22.1	25.4	1.8

[1]Computed by the negative compound interest formula (Lorimer 1981) from percentage of original population dying.

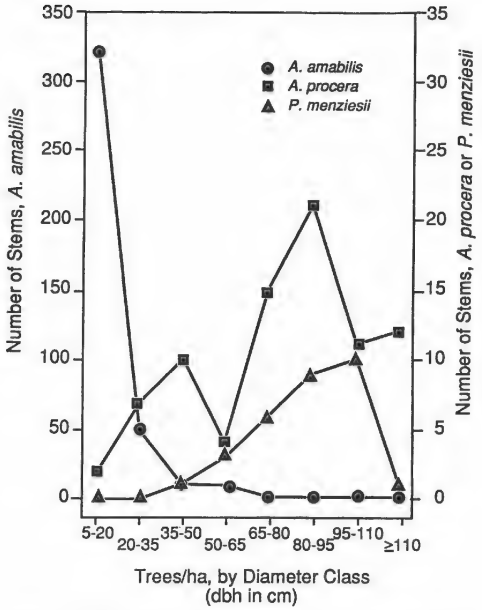

Figure 1. Diameter distribution in trees/ha for *Abies amabilis*, *A. procera*, and *Pseudotsuga menziesii* in 1977.

The most notable change between 1977 and 1993 was the decline of *A. procera* (Tables 1 and 2); the number of stems declined by 46.3 percent, and the basal area dropped by 41.5 percent. *A. amabilis* and *A. procera* accounted for most of the mortality (44% and 42% of dying stems, respectively, Table 1). Basal area lost to mortality was 7 times greater for *A. procera* than for *A. amabilis* (18.7 vs. 2.7 m^2/ha, Table 2).

More than half of the *A. amabilis* mortality was attributed to suppression or damage from falling green trees or limbs (Fig. 2); many dying *A. amabilis* were relatively small trees, with a median diameter at breast height (dbh) of 15 cm. Nearly all (98%) dying *A. amabilis* occupied lower canopy strata (*i.e.,* suppressed or intermediate trees (Daniel et al. 1979)). In contrast, almost 40 percent of the *A. procera* mortality was attributed to mistletoe or other pathogens (Fig. 2), more than to any other obvious cause. Eleven of the 13 trees with no recorded cause of mortality died standing, and it is likely that pathogens also contributed to the deaths of these trees. Most dying *A. procera* trees were relatively large (median dbh = 75 cm), and most (74%) occupied upper canopy strata (*i.e.,* codominant or dominant trees (Daniel et al. 1979)).

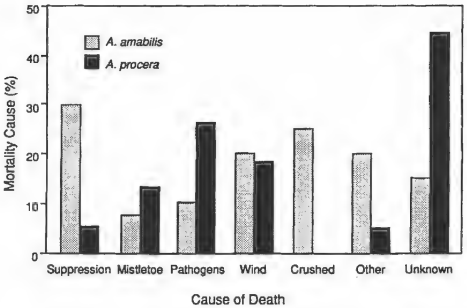

Figure 2. Causes of mortality for *Abies amabilis* and *A. procera* (1978–1993). Values displayed combine primary and secondary causes of mortality, and therefore add to more than 100% for each species.

Tests of Spatial Hypotheses

Neither quadrat- nor distance-based methods showed dying *Abies amabilis* to be significantly nearer to canopy trees than expected from a random distribution. Co-occurrence of dying *A. amabilis* and canopy trees alive in 1977 was not significantly different from random association at all quadrat sizes examined (Table 3). Furthermore, such co-occurrence was not unusually large in comparison with co-occurrence of the entire *A. amabilis* population and canopy trees (*i.e.,* randomization tests in Table 3). The combined count–distance method indicated that dying *A. amabilis* were not closer to canopy trees than either a random selection from the entire population of *A. amabilis* or a random selection of points for spatial scales from 1 to 30 m (Fig. 3).

Dying *A. procera* trees were aggregated according to both quadrat and combined count–distance methods, at least in comparison with random selections of points. However, aggregation of dying *A. procera* was not significant compared with the pattern of the entire population. Morisita's index indicated significant aggregation in 20 x 20 m quadrats, but not for other quadrat sizes (Table 4). However, compared with random samples from the entire population, the observed aggregation was not extreme (*i.e.,* P = 0.20 in randomization test, Table 4). The combined count-distance method indicated significant clumping at scales of 7, 8, 15–19, and 21 m in comparison with the random 95 percent confidence envelope (Fig. 4). However, in comparison with the random mortality 95 percent confidence envelope, dying *A. procera* were not aggregated at any scale from 1 to 30 m (Fig. 4).

TABLE 3. Tests of association between dying non-canopy *Abies amabilis* and canopy trees (all species) within quadrats of various sizes (2 x 2 contingency tables, tested with G-tests, except as noted).

Quadrat size (m)	G statistic	Adjusted G statistic	P	Randomization test[1] Average value of G statistic	Randomization test[1] P
1 x 1	0.91	0.66	P > 0.25	0.86	P = 0.87
2 x 2	0.03	0.03	P > 0.75	1.29	P = 1.00
5 x 5	0.09	0.09	P > 0.75	1.41	P = 0.73
10 x 10	0.13	0.12	P > 0.5	1.17	P = 0.73
20 x 20	0.00	N/A[2]	P = 1.0	0.00	P = 1.00

[1]Results from 1000 random samples of population of non-canopy *Abies amabilis* alive in 1977; P value is fraction of samples for which G statistic was at least as large as observed value.

[2]Probability computed by Fisher's exact test.

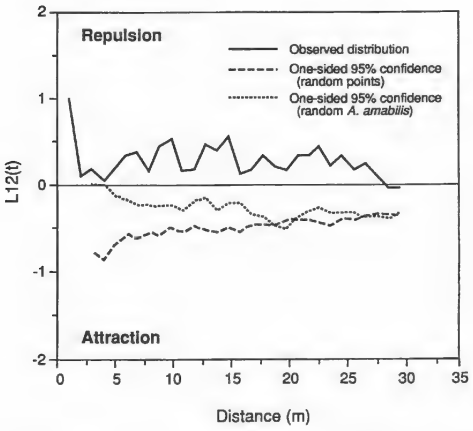

Figure 3. Bivariate combined count–distance analysis (L12(t) vs. t) for *Abies amabilis* dying between 1977 and 1993 and codominant and dominant trees in 1977. Solid line = observed distribution; dashed line = one-sided 95% confidence interval based on random selection of points ("random" confidence envelope); dotted line = one-sided 95% confidence interval based on random selection from initial population of *A. amabilis* ("random mortality" confidence envelope). Because of the discrete distribution of L12(t), neither confidence envelope could be computed for t = 1 or 2. Compared with both random sets of points and random selections from the initial population, P >> 0.05 for t =1 and 2.

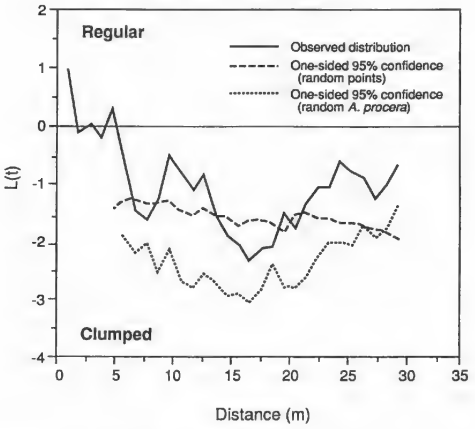

Figure 4. Combined count–distance analysis (L(t) vs. t) for *Abies procera* dying between 1977 and 1993. Line types as in Fig. 3. Because of the discrete distribution of L(t), the random and random mortality confidence envelopes could not be computed for t < 5 or 6, respectively. For all cases lacking 95% confidence envelope values, P >> 0.05.

TABLE 4. Values of Morisita's index, I_d, a test of aggregation of dying *Abies procera*.

Quadrat size (m)	I_d	P (1-tailed)	Randomization test[1] Average value of I_d	Randomization test[1] P
1 x 1	1.00	P = 1.0	0.00	P = 1.00
2 x 2	0.00	P = 1.00	1.67	P = 1.00
5 x 5	0.57	P = 1.00	0.49	P = 0.64
10 x 10	1.42	0.25 > P > 0.10	1.09	P = 0.22
20 x 20	1.35	P < 0.05	1.18	P = 0.20

[1]Results from 1000 random samples of population of *Abies procera* alive in 1977; P value is fraction of samples for which I_d was at least as large as observed value.

Discussion

Mortality in this study affected populations of two species that contrast in autecology. *Abies amabilis* in this stand is a tolerant, climax species (Dyrness et al. 1974; Crawford and Oliver 1990), as illustrated by its size distribution (Daniel et al. 1979). On the other hand, the size distribution of *A. procera* is typical of even-aged populations of intolerant species (Daniel et al. 1979) and is consistent with its status as a seral species (Dyrness et al. 1974; Franklin 1990). The usual agents of mortality also are different for the two species—falling trees and limbs and suppression affect *A. amabilis*, and pathogens affect *A. procera*. Thus, different spatial patterns of mortality were hypothesized for the two species: dying *A. amabilis* would be close to canopy trees, and dying *A. procera* would be aggregated.

Dying *A. amabilis*, however, were not closer than *A. amabilis* in general to canopy trees standing in 1977. Because toppling canopy trees contribute to mortality of *A. amabilis*, canopy trees may kill trees of lower strata at some distance from themselves. Thus the spatial pattern of small dying trees may more strongly reflect underlying processes when suppression, rather than physical damage from canopy trees, is the predominant cause of mortality. It is also possible that death of small *A. amabilis* trees in the study area is due more to crowding by neighboring trees of all sizes than to proximity to canopy trees (see, *e.g.,* Stohlgren 1993). The tendency of *A. amabilis* to establish in canopy gaps (Wilson 1991) could contribute to diminishing the influence of canopy trees on mortality of small *A. amabilis*. However, assessing the effects of crowding on small *A. amabilis* is beyond the scope of this study.

Although dying *A. procera* trees were aggregated at scale of about 20 m, dying trees were not more aggregated than the entire population. Death of adjacent *A. procera* may contribute to formation of large canopy gaps, but it is unclear whether proximity contributes to *A. procera* mortality. If patterns are to be definitively shown, future studies may need to encompass larger numbers of trees to compensate for non-random spatial distributions of *A. procera* (possibly caused by limited seed dispersal distances; see Franklin 1990). Even with larger sample sizes, it is conceivable that no aggregation of dying *A. procera* will be found. Published observations of spatial distribution of mortality due to root diseases of *Pseudotsuga menziesii* and other conifers in the Pacific Northwest indicate that either clumped or dispersed mortality may occur (Filip and Goheen 1995; Thies and Sturrock 1995).

Although the observed spatial patterns correspond to those hypothesized for *A. procera*, they did not correspond to those suggested for *A. amabilis*. In addition, based on the spatial pattern of all *A. procera* trees, the pattern of dying trees was not markedly different from randomness. The inferences that can be drawn from these results are limited by the relatively small study area and a lack of information on how representative the study area may be of *Abies* forests in the Pacific Northwest or any larger set of forests. Within those limitations, our results do not definitively support the proposition that the processes causing tree mortality can be deduced from spatial patterns of dying trees (though *cf.* Stohlgren 1993). Furthermore, these results indicate that it is sometimes not possible to predict spatial patterns of dying trees even when mortality causes are known.

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Ponderosa Pine Seedling Response to Planting-site Soil Fumigation and Fungicide Application

Abstract

Ponderosa pine (*Pinus ponderosa* Laws.) was used as a biological model to determine the effects of planting site soil fumigation and fungicide applications on stock planted in moderately-fertile soils of the Intermountain West of the United States. Five soil fumigation (Vapam) treatments, singularly and in combination with fungicide (triadimefon) applications, were compared to a control. Growth characteristics, nutrition, and ectomycorrhizal colonization were evaluated. Seedlings were significantly taller in the spring fumigation treatment at the end of four growing seasons. Greatest ectomycorrhizal colonization occurred in the non-fumigated treatment with fungicide applied before planting. Generally, spring or fall fumigation treatments, without fungicide applications, produced the tallest seedlings. These results suggest that soil fumigation applications before outplanting could improve early performance of ponderosa pine when reforesting sites with abundant, native ectomycorrhizal inoculum. It also suggests that if fumigation is impractical, reduction of vegetative competition may give similar growth gains. Elimination of non-native ectomycorrhizae in the nursery may improve colonization after outplanting.

Introduction

Ponderosa pine (*Pinus ponderosa* Laws.) is an important species on dry sites in the western U.S.A. (Linhart 1988). Rapid achievement of full stocking following harvesting is frequently difficult for ponderosa pine. Most regeneration failures in the western U.S.A. result from long periods of evaporative demand combined with low soil moisture during the growing season (Curtis and Lynch 1957). Low soil nutrient levels, particularly nitrogen (N), often compound moisture problems (Jurgensen et al. 1986). Competition from invading or residual plant regrowth after harvest can further reduce amounts of water and nutrients available to conifer regeneration (Miller 1987; Stewart 1974). Nonconifer vegetation that competes with tree crops for moisture can increase the risk of regeneration failure and reduce growth of established stands (Boyd 1985).

On sites with severe competition, common site preparation practices (i.e. scalping and burning) may not be adequate to reduce invading herbaceous species. These sites often must be replanted several times before stocking is adequate for stand development (Coffman 1982). Alternative methods to reduce seedling mortality and/or increase growth during early years may give foresters valuable options in treating and regenerating such sites. Options could include soil fumigation before planting and/or seedling treatment with fungicides before planting.

Soil fumigants are routinely used in bareroot forest tree nursery management to decrease weed competition, eliminate soil-borne pathogens, and reduce nematode infection (James et al. 1990; Tanaka et al. 1986). Fumigation usually results in superior seedling growth in nursery soils, which can continue after seedlings are outplanted (Benzian 1965; Danielson and Davey 1969; James et al. 1990; Thies and Patton 1971).

Klock (1980) used methyl bromide to fumigate planting spots during a field study in eastern Washington. Survival and growth of Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco) and ponderosa pine planted on these dry sites more than doubled compared to controls after 5 years. He speculated that fumigant-induced changes in soil biology affected disease resistance, soil nutrient availability, or ectomycorrhizal development, but detailed measurements were not taken (Bengtson and Smart 1981; Klock 1980).

In the western U.S.A., Vapam (sodium-N-methyl-dithiocarbamate) is often used as a soil fumigant in forest nurseries and may be more amenable for use in field outplanting situations since it does not require that the soil be covered with plastic after treatment. Vapam is less volatile than other fumigants, such as methyl bromide and is registered for fumigation of planting sites. While results were preliminary (first year), fumigation with Vapam produced Douglas-fir and western white pine (*Pinus monticola* Dougl. ex.

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D.Don) seedlings with increased root growth and total weight as compared to seedlings planted in non-fumigated soil. Vapam fumigation also eliminated competing vegetation (Cornwall 1985; Rainville 1987). However, changes in plant nutrition or ectomycorrhizal function were not measured.

Application of triadimefon, 1-(4-chlorophenoxy)-3,3-dimethyl-1-(1H-1,2,4-triazol-1-yl)-2-butanone, a systemic fungicide, inhibits ectomycorrhizal short root development in forest nurseries (South and Kelley 1982). However, Kelley (1987) noted that after 1 year, greenhouse-grown loblolly pine (*Pinus taeda* L.) seedlings treated with triadimefon had significantly more ectomycorrhizal short roots than control seedlings. Survival and growth of seedlings treated with triadimefon were similar to control seedlings after outplanting into plantations (Rowan and Kelley 1986).

Increases in growth that continue even after competing vegetation has reoccupied the site indicate a basic change in soil/tree root biology. Applying triadimefon in the nursery may encourage faster seedling root colonization by native ectomycorrhizal symbionts after outplanting to a forest site. Thus, soil sterilization as a method for competition control (both microbial and plant) and reduction of non-native ectomycorrhizae may have an additive effect and prove effective regeneration tools.

The objectives of this study were to: (1) examine the impact of planting-site fumigation with Vapam and fungicide applications of triadimefon on survival and growth ponderosa pine seedlings, and (2) determine seedling ectomycorrhizal colonization, height, diameter, and nutrition, and evaluate soil ammonium and nitrate levels in a moderately fertile, forested environment with high levels of native ectomycorrhizal inoculum.

Methods and Materials

Site Description

The study site is located at an elevation of 800 m on the Priest River Experimental Forest 19 km N of Priest River, ID, U.S.A. The previous stand which consisted of western white pine, Douglas-fir, lodgepole pine (*Pinus contorta* Dougl. ex Loud.) and western larch (*Larix occidentalis* Nutt.) was cleared in 1985 and the soil rototilled to a depth of 30 cm. The soil is a coarse, loamy, mixed frigid Typic Xerochrept (Soil Survey Staff 1975). Mean annual precipitation and temperature are 84 cm and 6.6° C, respectively. Approximately 80% of the precipitation falls as snow (Wellner 1976).

Study Design

A randomized complete block design was established on this site in 1988, with three replications of five treatments and an untreated control. Treatments consisted of:

(1) fall soil fumigation with Vapam[1],

(2) spring soil fumigation with Vapam,

(3) fall soil fumigation with Vapam and triadimefon applied to seedlings in the greenhouse before outplanting,

(4) fall soil fumigation with Vapam and triadimefon applied to seedlings in the greenhouse before outplanting plus four additional times throughout the first growing season,

(5) no soil fumigation and triadimefon applied to seedlings in the greenhouse before outplanting.

Seedlings treated with fungicide before planting (treatments 3, 4, and 5) had triadimefon applied three times at 2-week intervals, while actively growing in the greenhouse. Triadimefon was selected because of its suppressive effect on ectomycorrhizae development on pines (Marx and Cordell 1987). The concentration was 1.8 mg active ingredient/seedling mixed with a surfactant (Marx 1987). Plots were 30 m * 30 m in size with a 1 m buffer.

Soil Treatment Application

Fall and spring soil fumigations were achieved with 450 ml/m^2 of Vapam after the soil had been soaked to a depth of 30 cm by rain. Vapam was applied using a 10 liter watering can. Treated areas were water-sealed (surface soil soaked with water) to move the Vapam into the soil. Fall fumigation plots were treated the second week of October (1988). The soil was covered with black plastic until 4 weeks before spring planting. Spring fumigation plots were treated approximately 6

[1] The use of trade or firm names in this paper is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

weeks before planting (1989). The plots were covered with black plastic for 2 weeks, but were uncovered for 4 weeks before planting to allow the fumigant to dissipate. Control plots were covered at the same time spring fumigation plots were covered. Plots were covered with black plastic so they would be uncovered a uniform time before planting. Plots were tested for any remaining fumigant by planting highly sensitive tomato plants as an indicator 1 week before seedlings were outplanted. Plots were planted with 100 1-yr-old container-grown ponderosa pine seedlings on a 1-by-1 m spacing.

Seedling Sampling and Measurements

Before outplanting, 5 seedling root systems from each treatment were examined for ectomycorrhizal root tips. Active ectomycorrhizal root tips comprised approximately 10 percent of the root system in each treatment except the triadimefon treated seedlings which had none. After budset of the first and second growing seasons, 5 seedlings from each treatment and replication were carefully excavated. Top height, rooting depth, and root-collar diameter were measured. Tops of seedlings were severed from the roots, dried at 60° C for 24 h, weighed, and ground to pass a 20-mesh sieve. Seedling shoots (stem, branches, and needles combined) were prepared for analysis of Total N and phosphorus (P) by Kjeldahl digestion methods using the salicylic acid-sodium thiosulfate modification (Bremner and Mulvaney 1982). They were analyzed on an Alpkem Rapid Flow Analyzer II Model 300. Calcium (Ca) and magnesium (Mg) were analyzed by atomic absorption spectroscopy, potassium (K) was analyzed by flame emission after samples had been dry ashed at 450° C and leached with 2N HNO_3. After seedling roots were washed, total ectomycorrhizal tips were counted with a 20x binocular microscope. Roots were subsequently dried at 60° C for 24 h and weighed.

Soil Sampling and Analysis

Five 20 g random soil core samples were collected to a depth of 15 cm in each treatment replication 1 d before fumigation, and 14 and 45 d after fumigation. They were sieved to pass a 2 mm screen. Control soil samples were collected at the same time as the fall fumigation samples. Undried soil samples were extracted using 1N KCl and analyzed for ammonium-nitrogen and nitrate-nitrogen using an Alpkem Rapid Flow Analyzer II Model 300 (Keeney and Nelson 1982).

Statistical Analysis

The significance of difference among treatments was tested using a one-way analysis of variance (ANOVA) for a randomized complete block design followed by Scheffe's multiple range test (Scheffe 1953). A type I error rate of $p \leq 0.05$ was applied.

Results and Discussion

Seedling Growth Characteristics

After the first growing season, height growth was greatest in the fumigation only treatments, and least in the fall fumigation treatment with continuous triadimefon application (Table 1). Rooting depth through year four was unaffected by these treatments (data not shown). Survival after the first growing season was 70% in the control, 71% in the no fumigation-triadimefon treatment, 85% in the fall fumigation and continuous triadimefon treatment, 87% in the fall fumigation pre-plant triadimefon treatment, 90% in the fall fumigation treatment, and 96% in the spring fumigation treatment. Root-collar diameter was greatest in the fumigation only treatments. Second-year seedling growth was similar to the first year. Seedlings growing in the fumigated treatments had greater height growth, root growth, diameter, and biomass than the other treatments, but, as with the first-year, the differences were not always significant. By the end of the fourth season the seedlings growing in the spring fumigation plots had significantly greater height than those in the other treatments (Table 2).

Spring fumigation before outplanting may provide the necessary environment (i.e. control of resident fungi adversely affecting root systems) for improved seedling growth. Fall fumigation may allow recolonization of the soil before spring outplanting. Other investigators have noted striking increases in seedling height and biomass in fumigated soil compared to controls that were not fumigated (Anderson and Liberta 1992; Cornwall 1985; Henderson and Stone 1970; James et al. 1990; Klock 1980; Rainville 1987).

The cost of using Vapam across an entire site may be prohibitive ($2470/ha) (Landis and Campbell 1989). However, soil fumigation as a

TABLE 1. Growth characteristics of ponderosa pine seedlings as affected by site treatment one and two years after treatment. (n=20 for year 1 and n=20 for year 2)

Treatment	Year 1 Height (cm)	Year 1 Caliper (mm)	Year 1 Total Biomass (g)	Year 2 Height (cm)	Year 2 Caliper (mm)	Year 2 Total Biomass (g)
Spring fumigation	18.1a (0.3)[B]	4.7ab (0.2)	6.0ab (0.4)	36.1a (0.9)	12.7a (0.4)	49.9a (3.2)
Fall fumigation	18.1a (0.3)	5.2a (0.2)	6.1a (0.4)	33.5ab (0.9)	11.9a (0.4)	45.7ab (3.2)
Fall fumigation and triadimefon	17.6ab (0.3)	4.5abc (0.2)	6.2a (0.4)	32.3b (0.9)	11.7a (0.4)	41.4ab (3.3)
Fall fumigation and continuous triadimefon[A]	16.8b (0.3)	4.6ab (0.2)	5.7ab (0.4)	32.7ab (0.9)	11.8a (0.4)	42.1ab (3.2)
No fumigation and triadimefon	17.4ab (0.3)	3.8c (0.3)	5.1b (0.3)	30.8b (0.9)	10.0b (0.4)	34.9b (3.3)
Control	17.6ab (0.4)	4.4bc (0.3)	5.2b (0.4)	33.2ab (0.9)	11.8a (0.4)	42.9b (3.2)

[A]Continuous triadimefon during year 1 only.

[B]Different letters indicate significant differences ($p \leq 0.05$) among treatments. Values in parentheses are standard error of the mean.

TABLE 2. Height of 4-year-old ponderosa pine seedlings as affected by site treatment (n=250).

Treatment	Height (cm)
Spring fumigation	74.8a (0.8)[B]
Fall fumigation	68.5b (0.9)
Fall fumigation and triadimefon	68.5b (0.9)
Fall fumigation and continuous triadimefon[A]	64.9b (0.9)
No fumigation and triadimefon	60.6c (0.9)
Control	68.1b (0.9)

[A]Continuous triadimefon during year 1 only.

[B]Different letters indicate significant differences ($p \leq 0.05$) among treatments. Values in parentheses are standard error of the mean

site preparation technique in the western U.S.A. could be used on certain problem sites which have a long history of regeneration failure or inadequate seedling establishment.

The lack of many significant differences between treatments and controls during the first growing season may be due to outplanting nursery stock with pre-set buds and a high nutrient status (Kozlowski et al. 1973). The growth changes in fumigated soil treatments may be at least partially associated with altered populations of soil microbes or a reduced level of weakly pathogenic fungi (fungi that slowly deteriorate root systems) (James et al. 1990; Munnecke et al. 1978; Smith and Bega 1966). Although no biomass measurements of herbaceous competition were taken, visual assessment indicated the fumigated plots had substantially less competition than plots that were not fumigated. This may also contribute to growth increases. More moisture may have been available for seedling uptake.

By the end of the second year, seedlings that had triadimefon applied, either before planting or continuously, had reduced height growth, root-collar diameter and total biomass compared to the fumigation treatments. Marx (1987) and Rowan and Kelley (1986) found no significant effects of triadimefon on first-year growth of nursery-grown bareroot loblolly or slash pine seedlings compared to control seedlings. However, Davis (1991) found that triadimefon can act as a potent inhibitor of shoot growth with effects persisting for several years.

Ectomycorrhizae Colonization

There were no significant treatment differences during the first year in total ectomycorrhizal root tips between treatments (Table 3). This is consistent with results from the southeastern U.S.A.

TABLE 3. Total ectomycorrhizal short root (EMSR) colonization and EMSR/gram of dry root of ponderosa pine seedlings one and two years after site treatment. (n=20 for year 1 and n=20 for year 2)

Treatment	Year 1		Year 2	
	Total EMSR	EMSR/gram of dry root	Total EMSR	EMSR/gram of dry root
Spring fumigation	30a (4)[B]	15b (3)	32b (6)	3a (2)
Fall fumigation	28a (4)	13b (2)	42ab (6)	8a (2)
Fall fumigation and triadimefon	31a (4)	20b (2)	39ab (6)	4a (2)
Fall fumigation and continuous triadimefon	24a (4)	10b (30)	59a (6)	8a (2)
No fumigation and triadimefon	49a (4)	36a (3)	62a (6)	9a (2)
Control	32a (4)	22ab (3)	42ab (6)	5a (2)

[A]Continuous triadimefon during year 1 only.

[B]Different letters indicate significant differences ($p \leq 0.05$) among treatments. Values in parentheses are standard error of the mean.

where increasing rates of triadimefon did not alter first year ectomycorrhizal colonization of feeder roots (Kelley 1987). However, ectomycorrhizal root tips per gram of dry root were significantly greater in the no fumigation, before planting, triadimefon application treatment compared to the others. This is probably related to the slightly greater number of total ectomycorrhizal tips on these seedlings. In this study, fumigation alone did not improve ectomycorrhizal colonization of ponderosa pine. In fact, soil fumigation has been shown to reduce populations of ectomycorrhizal fungi (Johnson and Zak 1977). Interestingly, suppression of ectomycorrhizae in the nursery and during the first growing season by triadimefon resulted in a general increase in total ectomycorrhizal tips the second growing season. However, on seedlings that were not reinoculated with ectomycorrhizae or without large native populations of ectomycorrhizae available, colonization can be slow (Henderson and Stone 1970).

Triadimefon may rid seedlings of non-site-specific ectomycorrhizae early in the first growing season and allow site-specific ectomycorrhizae to colonize roots more vigorously (Harvey et al. 1991; Page-Dumroese et al. 1990). Although triadimefon suppresses ectomycorrhizae development on pines (Marx and Cordell 1987), it appears that maximum seedling growth can be achieved with a moderate number of native ectomycorrhizae. In this study, greater ectomycorrhizal colonization did not translate into greater seedling biomass.

Seedling Nutrition

Seedling nutrient concentrations did not always correspond to seedling growth characteristics. After the first growing season, seedling K concentration among treatments was unchanged (Table 4). In the fall fumigation treatment with triadimefon applied before planting, Mg concentrations were greatest compared to most other treatments, except the no fumigation triadimefon treatment before planting. Results were similar for Ca. Greater concentrations of Ca and Mg in triadimefon-treated seedlings may be caused by residual triadimefon and its metabolite triadimenol in the needles. After foliar application of triadimefon, it remains in the sprayed portion of the plant and is usually not redistributed except for movement to the leaf margins (Davidse and DeWaard 1984). Triadimefon has been shown to reduce transpiration and produce thicker, darker leaves on many plants (Fletcher and Nath 1984).

While there were significant differences in first year total seedling P, the actual values differed by very little and are probably not biologically significant. By the end of the second year differences were no longer important. Because endemic ectomycorrhizae were likely eliminated from the fumigation plots, we expected that seedling P would be depressed (Anderson and Liberta 1992; Henderson and Stone 1970). Apparently, in this soil type, P was available in sufficient quantity for normal seedling uptake.

TABLE 4. Nutrient concentrations of combined ponderosa pine seedling foliage and stems one and two years after site treatment. (n=20 for year 1 and n=20 for year 2).

Treatment	Year 1					Year 2				
	Total N	Total P	Ca	Mg	K	Total N	Total P	Ca	Mg	K
	------(percent)------		---------(up/g)--------			------(percent)------		---------(ug/g)---------		
Spring fumigation	0.79a	0.10ab	2168a	894b	5464a	1.78a	0.35a	1863c	813a	5757a
	(0.05)[B]	(0.06)	(192)	(87)	(55)	(0.32)	(0.03)	(112)	(40)	(280)
Fall fumigation	0.81a	0.10ab	2325ab	905b	5076a	1.73a	0.45a	1982bc	823a	5279a
	(0.05)	(0.06)	(174)	(79)	(50)	(0.31)	(0.03)	(106)	(40)	(265)
Fall fumigation and triadimefon	0.76ab	0.09b	2565a	1145a	4937a	1.72a	0.36a	2042bc	848a	5416a
	(0.04)	(0.05)	(161)	(73)	(46)	(0.32)	(0.03)	(111)	(42)	(276)
Fall fumigation and continuous tridimefon[A]	0.78ab	0.10ab	2124b	884b	5386a	1.55b	0.36a	2241a	849a	5528a
	(0.05)	(0.06)	(174)	(79)	(50)	(0.35)	(0.03)	(121)	(45)	(301)
No fumigation and triadimefon	0.69b	0.10ab	2358ab	982ab	5009a	1.68ab	0.37a	2153ab	809b	5484a
	(0.05)	(0.06)	(192)	(87)	(55)	(0.33)	(0.03)	(112)	(42)	(281)
Control	0.76ab	0.11a	2045b	859b	5146a	1.77a	0.39a	2021bc	836a	5694a
	(0.04)	(0.05)	(165)	(75)	(47)	(0.31)	(0.03)	(107)	(40)	(268)

[A]Continuous triadimefon during year 1 only.

[B]Different letters indicate significant differences ($p \leq 0.05$) among treatments. Values in parentheses are standard error of the mean.

Ponderosa pine total N was greatest in the two fumigation-only treatments. Second-year fall fumigation with continuous first year triadimefon had the lowest total N values. This may be due to the plant growth-regulating properties of triadimefon (Davis 1991; Fletcher and Nath 1984). Wang et al. (1986) reported that triadimefon applications increased the mineral nutrition of apple seedlings. Most differences associated with triadimefon applications have likely been caused by variations in application rates and frequencies or by variations in environmental conditions. Soil fumigation has been shown to increase tree nutrient uptake (Benzian 1965). In this study, fumigation alone slightly increased seedling N concentrations during the first growing season. However, second year results indicate that total N was not different from the controls.

Soil N Transformations

Although there was an immediate increase in ammonium-N in fumigated soils, levels had dropped off to near those before fumigation levels by 45 d after fumigation (Fig. 1). Spring fumigation was the only treatment with significantly higher ammonium at planting time. Higher concentrations in the spring fumigation treatment may be attributed to warm soil temperatures immediately after fumigation. The short elapsed time between fumigation and planting in this treatment may have allowed seedlings to capitalize on N releases. This likely contributed to the improved seedling growth in this treatment. Similar results are reported elsewhere (Munnecke and Ferguson 1960; Singha et al. 1979).

Soil nitrate-N levels followed the same trend as ammonium-N, with the spring fumigation treatment having the highest concentration at planting time (Fig. 2). Other studies have shown that fumigation had a strong, initial effect of depressing nitrification (Munnecke and Ferguson 1960; Singha et al. 1979). The toxic effect of Vapam on nitrifiers has been attributed to the highly toxic compound methyl isothiocyanate (Tu 1972). This was apparently not the case here since fumigation rates were low and Vapam was watered into the soil after application and its toxicity may have been reduced.

Conclusions

Fumigation offers an effective way to rid a site of all competition by controlling both vegetation and microorganisms in the rooting zone. This treatment alone provides an environment conducive for enhanced regeneration performance. Spring fumigation provides the greatest opportunity for improving ponderosa pine seedling growth,

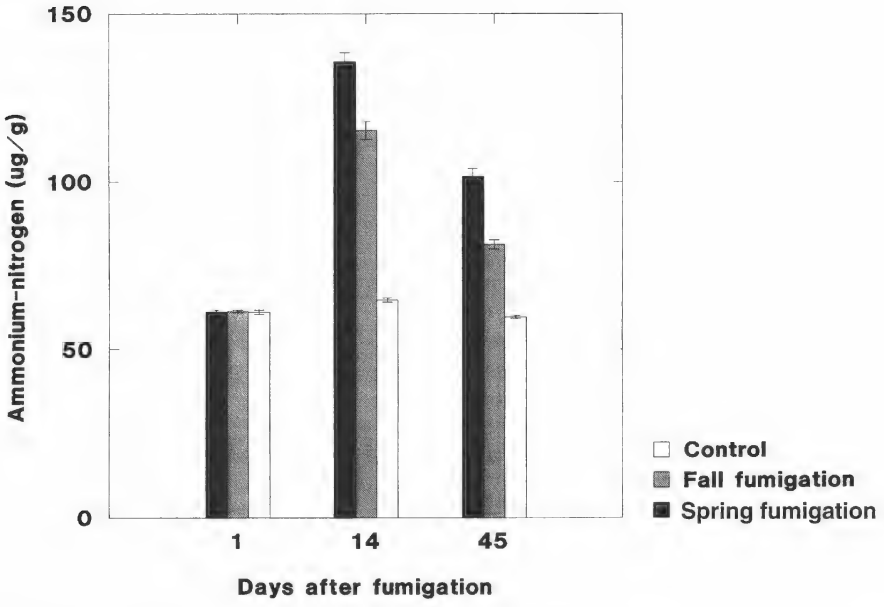

Figure 1. Change in soil ammonium-N levels 1, 15, and 45 days after fumigation with Vapam. Error bars indicate 95% confidence intervals around the mean.

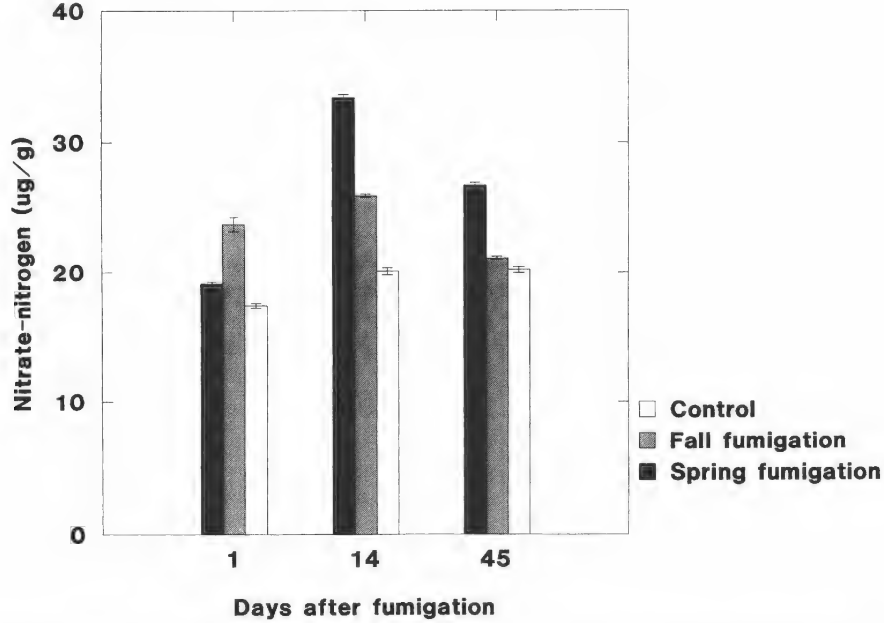

Figure 2. Change in soil nitrate-N levels 1, 15, and 45 days after fumigation with Vapam. Error bars indicate 95% confidence intervals around the mean.

however fall fumigation was also successful. Fall fumigation may be more effective if seedlings are planted 4 to 6 weeks after the fumigation instead of the following spring. However, fall weather in the western U.S.A. is often unfavorable to either fumigation or planting. Initial growth increases from fumigation, particularly if conducted in the spring prior to planting, appear to last well beyond the first growing season.

While mechanical site preparation and burning may be the standard tools of a land manager, fumigation might provide a viable alternative for successful regeneration on harsh sites with abundant competition. Fumigation is a method that can increase seedling survival and growth immediately after planting, a characteristic potentially extremely valuable when reforesting harsh sites.

Eliminating ectomycorrhizae before planting, or during the first growing season, enhanced second year colonization, but seedling growth was not improved over moderate colonization levels. Use of triadimefon to eliminate ectomycorrhizae in the nursery is likely to be helpful if rapid colonization by native ectomycorrhizae is essential for seedling survival and if there is abundant, native inoculum.

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Endangered, Threatened, and Sensitive Plants of Fort Lewis, Washington: Distribution, Mapping, and Management Recommendations for Species Conservation.

Abstract

The loss of native species and their habitats has increased with urban development, agriculture, and resource utilization. According to the Washington Natural Heritage Program, 20 plants listed as endangered, threatened, or sensitive are suspected to occur on the glacial outwash soils of south Puget Sound. In our study, more than 3,000 ha of prairie, wetland, and moist-forest plant communities were systematically sampled at Fort Lewis, Washington, and rare plant species, their habitats, and associated species were mapped. Four rare species, *Aster curtus*, *Trillium parviflorum*, *Carex comosa*, and *C. interrupta*, were found. *Aster curtus*, the most abundant of these four species, attained highest cover and frequency on prairies dominated by *Festuca idahoensis*, other graminoids, and native forbs. It also was present on some sites dominated by trees or non-native species. *Trillium parviflorum* was found in moist-forest communities with an overstory of conifers and hardwoods. *Carex comosa* was found on the margins of two wetlands, and *C. interrupta* was found growing on a gravel bar of the Nisqually River. Major threats to the four rare species are discussed, and recommendations are made for management of rare plant habitats with the goal of preserving the species.

Introduction

In the south Puget Sound lowlands of western Washington, prairies, shallow lakes and wetlands within a conifer-dominated landscape were formed on the coarse gravel deposits from the Vashon glacier. A high diversity of plant species and plant communities is characteristic of these habitats. However much of the Puget Sound lowland is currently used for urban development, agriculture, and resource extraction (gravel mining, timber, water). Impacts to habitat by these activities or by recreational trampling are a major threat to plants and plant communities.

One of the largest tracts of relatively undisturbed forests, wetlands, and prairies in the Puget Sound lowlands is on the Fort Lewis Military Reservation (FLMR), a U.S. Department of Army (DoA) installation located between Tacoma and Olympia, Washington. The DoA and all Federal land managers are directed by the Endangered Species Act of 1973 to protect and conserve the habitat of endangered, threatened, sensitive, and candidate (ETS) species on its reservations. The terms "endangered," "threatened," and "sensitive" used in this paper follow the designations established by the Washington State Department of Natural Resources, Natural Heritage Program (WNHP). Endangered plant status is assigned to a vascular plant taxon in danger of becoming extinct or extirpated in Washington. A threatened plant taxon is likely to become endangered within the near future in Washington if factors contributing to population decline or habitat degradation or loss continue. Sensitive plant taxa are vulnerable or declining and could become endangered or threatened in the State without active management or the removal of threats (WNHP 1994). Candidate species applies to taxon that are being considered for listing under the Endangered Species Act of 1973, as amended.

Currently, 20 species of ETS plants occur or potentially occur in the south Puget Sound lowlands (WNHP 1994). One, *Aster curtus*, is currently designated a species of concern by the U.S. Fish and Wildlife Service (1996). This designation suggests a threat to the persistence of the species but requires additional data for formal listing as threatened or endangered.

During spring and summer of 1992 and 1993, we undertook an inventory of ETS plant species at FLMR. We had five objectives:

(1) Map the distribution of ETS plant species within the FLMR;

(2) Describe the habitats and plant species associated with ETS plant species;

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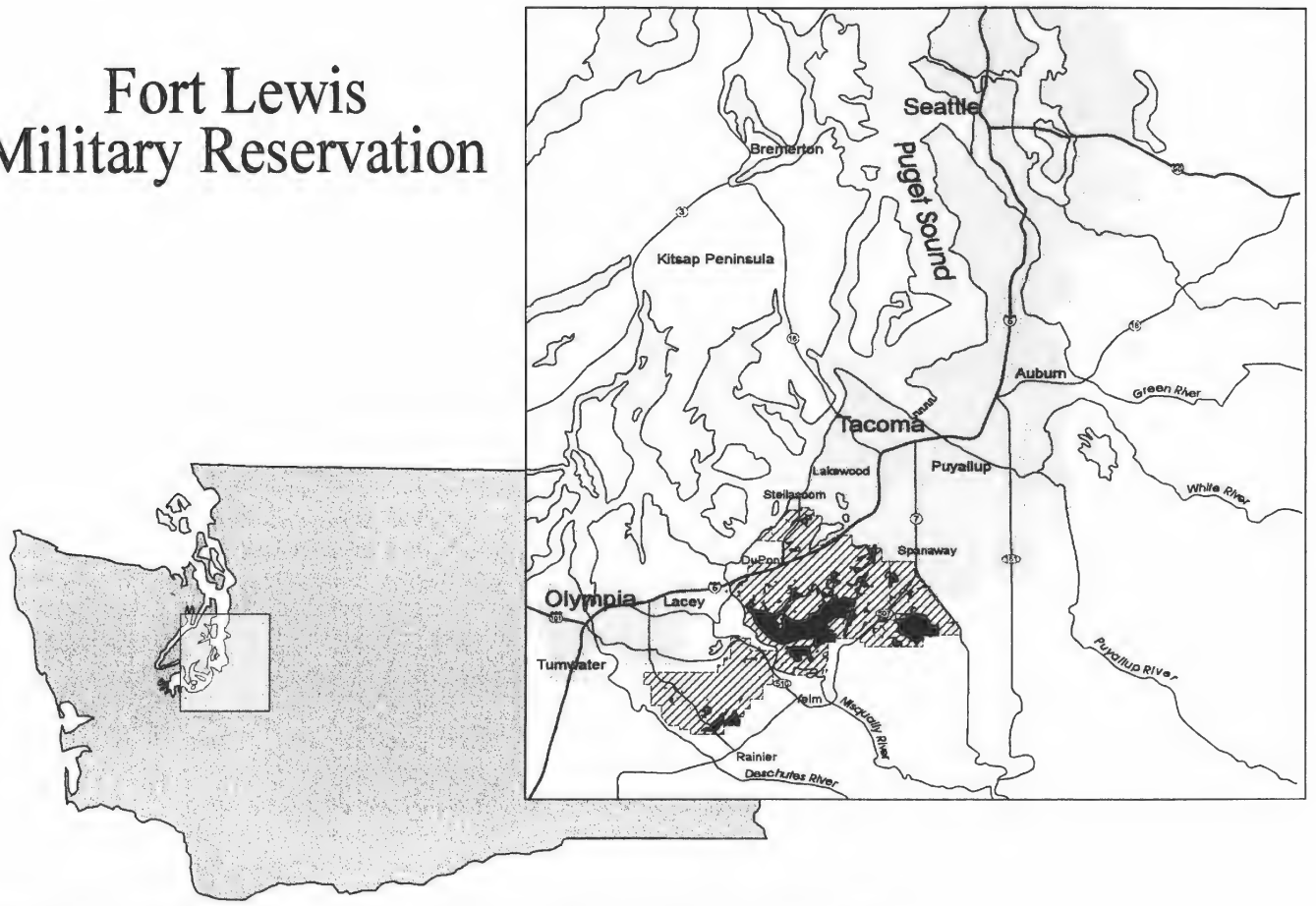

Figure 1. The location of Fort Lewis in the southern portion of Puget Sound, Washington. Prairies are shown in dark gray.

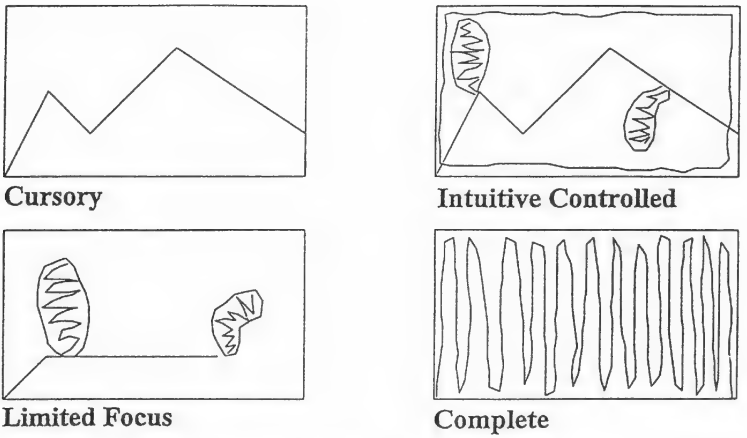

Figure 2a. Sensitive plant search methods used in 1992. Rare plant data were collected in selected habitat suspected to contain the rare species. A hierarchical approach ranging from a cursory reconnaissance of the habitat to a complete examination of the entire area and its perimeter were used to search for rare taxa.

(3) Describe habitats and plant communities in areas that were inventoried but revealed no ETS plant species;

(4) Identify the threats to ETS plant species and make management recommendations to protect populations on the FLMR;

(5) Determine future research needs.

Description of Study Area

The FLMR covers 34,818 hectares (86,000 acres) and is located in the southern portion of the Puget Trough (Figure 1). The landforms and soils of present-day FLMR were formed by the Vashon Glacier that retreated from the area 14,000 years ago and by subsequent erosion and the action of rivers (Kruckeberg 1991). Soils are derived from glacial till and drift and are well drained. The topographic relief is moderate, with elevation ranging from sea level to 173 m. Annual precipitation averages 100 cm at the Gray Airfield weather station, FLMR (unpublished data). The plant communities of FLMR are diverse. Our inventory of ETS plants included large tracts of prairie, wetlands, moist-conifer forests, and oak woodland habitat (3,036 hectares).

Methods

To determine which of the 20 ETS plant species of the Puget Trough might be present on FLMR, we examined the WHNP element occurrence database for historical records of species occurrences in Thurston and Pierce counties. We assembled data on species descriptions, habitats, phenology, and nomenclature from Hitchcock and Cronquist (1973), the WNHP Information System, local amateur and professional botanists familiar with habitats of Fort Lewis, and botanists from the USDA Forest Service, Washington Department of Natural Resources, and environmental consulting firms. Of the 20 ETS species potentially occurring on the FLMR, two were known to be associated with wetlands, four with bogs, three with moist-forests, three with riparian areas, two with forest openings, four with prairies, and two with steep, forested bluffs along Puget Sound. Then, we located these habitat types on 1:12,000 aerial photographs and transferred them to 1:24,000 USGS quad maps or orthophoto quads for field work.

During 1992, we revisited sites of historical occurrences and conducted reconnaissance surveys of prairies, wetlands, moist conifer forests, and oak woodlands by using a hierarchial approach (Figure 2a) to first identify suitable habitats and then to search for ETS plants:

(1) **Cursory**—a quick (15-30 min/ha), reconnaissance of an area to determine if it appeared to be suitable habitat or to assess the phenological development of the plants.

(2) **Limited focus**—a close examination of selected areas within potential habitats but not a search of the entire selected area.

(3) **Intuitive controlled**—a close examination of specific areas of potential habitat as well as a careful search of the perimeter of the potential habitat.

(4) **Complete**—a complete examination made by walking parallel transects throughout the entire area and its perimeter. This method was used if the area appeared to be optimal habitat for the target species.

During 1993, we systematically sampled plant species diversity with transects (Figure 2b). The four lines of the transect formed a box with three plots 50 m apart on each leg of the box. The entire box covered an area of 2.25 ha. Transects were randomly located in relatively homogeneous areas of forest, wetland, and prairie communities. Prairie communities on FLMR had been classified into three types (Rex Crawford, WNHP, personal communication): (1) prairies that had >50% total cover of native species, including >10% cover of *Festuca idahoensis* and <10% cover of alien species (native prairies); (2) prairies that had >50% cover of native species, 10-50% cover of alien species, and <10% cover of *F. idahoensis* (mixed prairies); and (3) prairies that had >50% cover of alien species, <10% cover of *F. idahoensis* (alien-dominated prairies). We categorized the prairies we sampled using Crawford's classes.

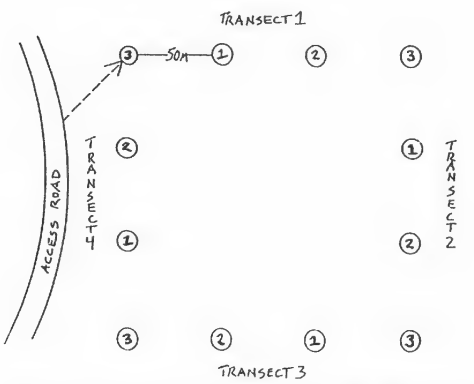

Figure 2b. Plant sampling method used for biodiversity studies in 1993. Rare plant data were collected for ETS plants that were encountered in plots, en route to plots, and on and off lines between plots. The start point for plot 1 was randomly selected.

We recorded percentage cover and average height for all species found in each plot. Species cover estimates were recorded as trace = 0.5%, 1 to 10% in 1-percent increments and 15 to 100% in 5-percent increments. Height was recorded to the nearest decimeter. We used Hitchcock and Cronquist (1973) to identify plants in the field. Voucher specimens of all species encountered were collected, and identifications were confirmed at the Olympia Forestry Sciences Laboratory, Pacific Northwest Research Station (USDA Forest Service), and the Botany Department Herbarium, University of Washington, Seattle. Nomenclature used in the text and tables is from Kartesz (1994).

ETS plant species found within the sampling box or while walking from one plot to the next were recorded on a ETS-plant sighting form and mapped. We also determined the number of aerial stems in the population and the area covered by the individual or population. The life-history stage of the ETS plant was recorded as vegetative, flowering, fruiting, or senescent. The pattern of distribution of ETS plants was determined to be clumped (in discrete patches), scattered-random, or scattered-even. *Aster curtus,* for example, was found clumped in numerous patches distributed over large areas. We estimated the number of individuals in each patch and the number of patches.

For each ETS plant population we found, we dug a shallow soil pit (25 cm deep) to determine the texture of the soil and the percentage of cobble and rocks. Aspect and slope were recorded.

Results

We searched for 20 potential ETS species (Figure 3) and found 97 populations (Table 1, Figures 4-8) of four ETS species during 1992 and 1993: *A. curtus, Trillium parviflorum, Carex comosa*, and *C. interrupta*. In addition to confirming historical records of *A. curtus* and *T. parviflorum* (Severinghaus and Goran 1981, Sheehan and Clampitt 1984, Gilbert et al. 1991), we found several new populations of *A. curtus* and *T. parviflorum*. Small populations of *C. comosa* and *C. interrupta*, species not previously known to occur on FLMR, also were discovered.

Species Accounts

Aster curtus

Species description. Aster curtus is an herbaceous perennial that grows from a slender, creeping

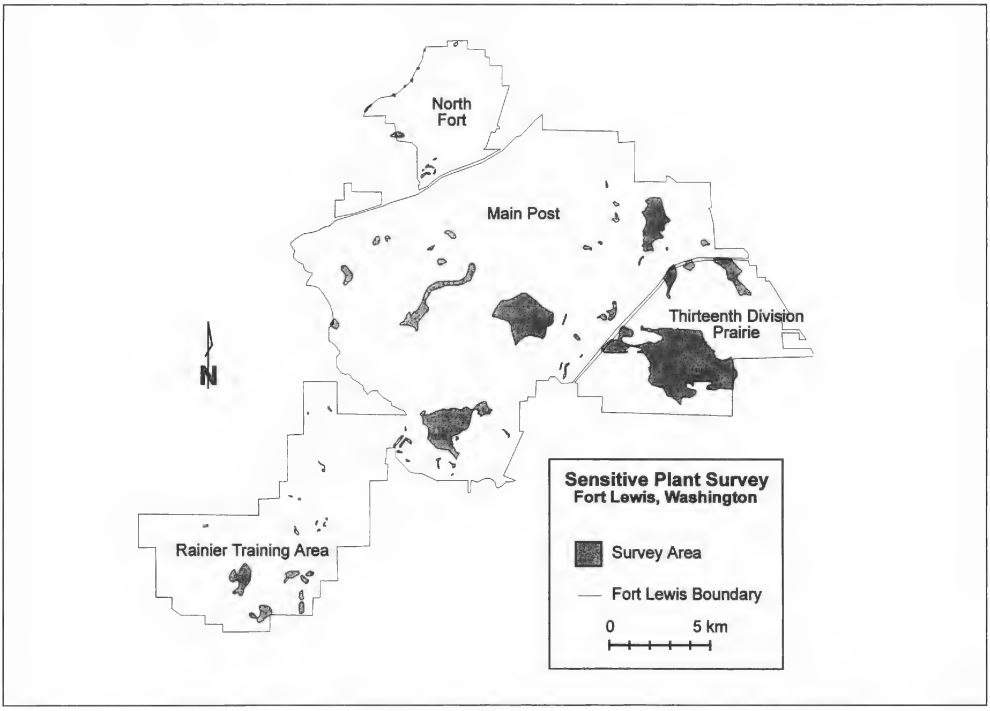

Figure 3. The location of sensitive plant surveys at Lewis, WA. A total of 3036 hectares was sampled for rare plants.

TABLE 1. Rare plant species found on Fort Lewis Military Reservation, WA. Occurrence by habitat, number of occurrences, and area (hectares) covered by each species. Rare plant searches and sampling was undertaken on 3036 hectares total.

Species	Habitat	Number of occurrences	Area (ha)
Aster curtus	Prairie, prairie-margin woodlands	73	190
Tillium parviflorum	moist forests	21	10
Carex comosa	wetland	2	0.14
Carex interrupta	gravel bar	1	0.05

rhizome and produces short (1-3 dm), erect stems with a compact, terminal cluster of flowering heads atop each stem (Hitchcock et al. 1969). Plants generally produce flowers and fruits in August and September, although achenes may persist on some plants into October. Achenes bear a pappus of short, capillary bristles that facilitates wind dispersal of seed. A regional endemic, this species occurs only on low-elevation prairies west of the Cascade Range, from Vancouver Island and the Puget Trough south into the Willamette Valley, Oregon (Meinke 1982). *Aster curtus* is classified as sensitive in Washington (1994) and is designated as a species of concern in the 1996 Federal Reigster Review of Plant and Animal Taxa.

Habitat and associated species. Aster curtus occurs primarily on open to partially wooded prairies, characterized by >50% cover of native species. *Festuca idahoensis*, *Eriophyllum lanatum*, *Solidago spathulata* var. *neomexicana*, and *Arctostaphylos uva-ursi* had the greatest cover and were the most frequently encountered associated species (Table 2). We often found *Pinus ponderosa* and *Quercus garryana* as overstory associates; however, *A. curtus* cover was less abundant

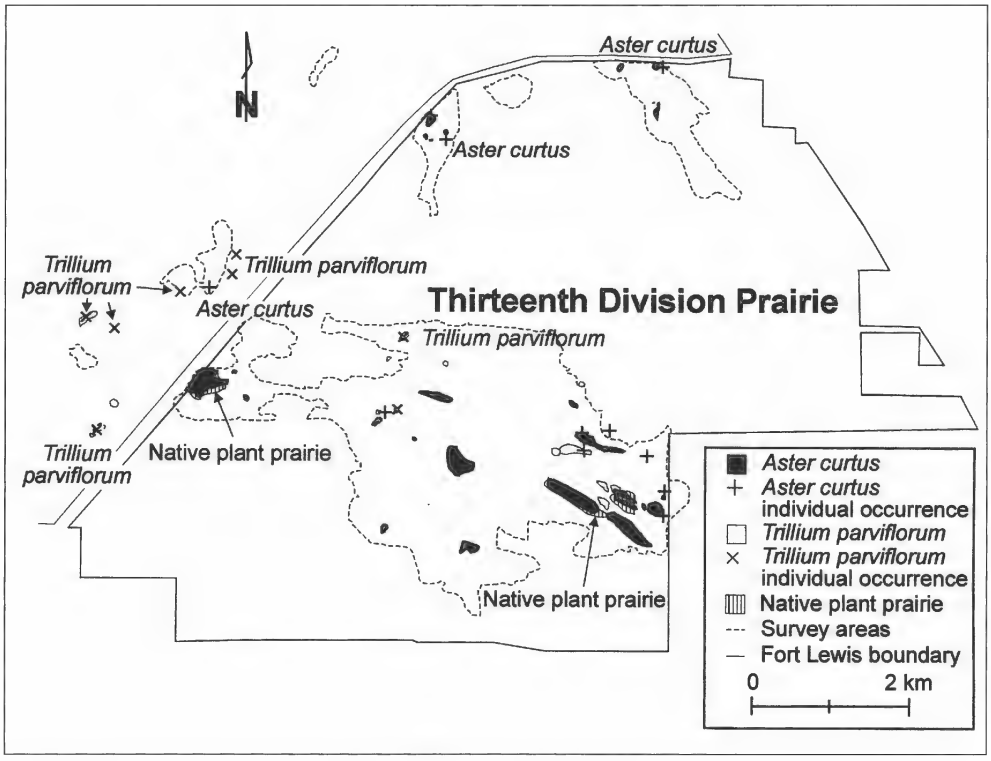

Figure 4. The location of *Aster curtus* and *Trillium parviflorum* on the 13th Division prairie.

under a tree overstory than under open prairie conditions.

We also found *Aster curtus* at sites on the Fort Lewis prairies harboring non-native plant species: *Cytisus scoparius*, *Agrostis tenuis*, *Hypochaeris radicata*, *Leucanthemum vulgare*, *Hypericum perforatum*, and *Plantago lanceolata* (Table 3). Native species, such as *Pseudotsuga menziesii*, are invading prairie habitat as a successional process; on prairies where *P. menziesii* was found, cover of *Aster curtus* was lower than on open prairies.

Pattern of abundance. We always found *A. curtus* at lower cover and frequency on alien-dominated prairies than on native or mixed-composition (native and alien) prairies (Tables 2 and 3). Because of its rhizomatous habit, *A. curtus* always occurred in clumps. It was found in trace amounts on alien-dominated prairies but had a frequency of >25 % on prairies dominated by *Hypochaeris radicata*/*Plantago lanceolata*/litter and *Agrostis tenuis*/*Cytisus scoparius*/cryptogam plant communities. Canopy cover above *A. curtus* ranged from full sun on open prairies to 30% shade from shrubs or overstory trees on prairies invaded by non-native shrubs or *P. menziesii*.

On the native-species-dominated prairies, *A. curtus* was found in scattered patches containing 16 to >10,000 stems per patch. Patch size ranged from 1 to 40 m^2, with an average patch size of 10 m^2. On portions of two near-pristine prairies (13th Division, Figure 4; and Johnson Prairie, Figure 8), more than 30 distinct patches of *A. curtus* with total stem counts of >200,000 shoots were found. On Johnson Prairie and the far west portion of 13th Division Prairie, *A. curtus* covered about 1% of the total prairie habitat, with cover up to 21% in some sampling plots.

Topography and soils. All populations of *A. curtus* occurred on relatively broken topography

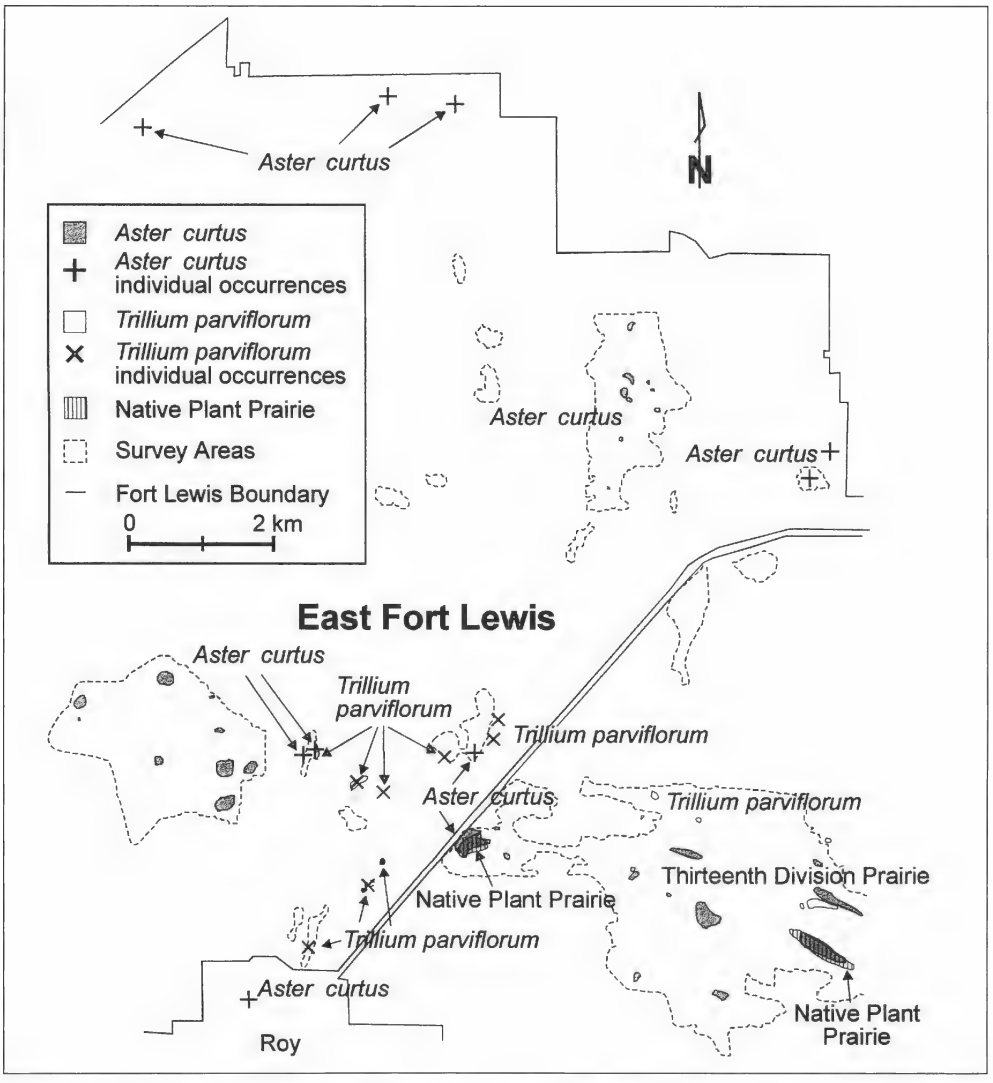

Figure 5. The location of *Aster curtus* and *Trillium parviflorum* populations and individual plants on East Fort Lewis.

(mounds, small rises, and swales). This feature is uncommon to most FLMR prairie topography, which was usually flat or gently undulating. Soils had deep (20-50 cm) organic horizons over well-drained, gravelly, glacial outwash.

Phenology. Fruits and flowers were observed on about 30% of the stems in each patch. Reproductive structures were not found on stems under 10 cm in height. A trace (<1%) of observed stems appeared senescent (all leaves brown and withered), and the majority (70%) were found in vegetative stage.

Trillium parviflorum

Species description. *Trillium parviflorum* is a perennial herb that produces a single, erect annual stem from a short, stout rhizome. The stem is naked, with three ovate, round-tipped, green

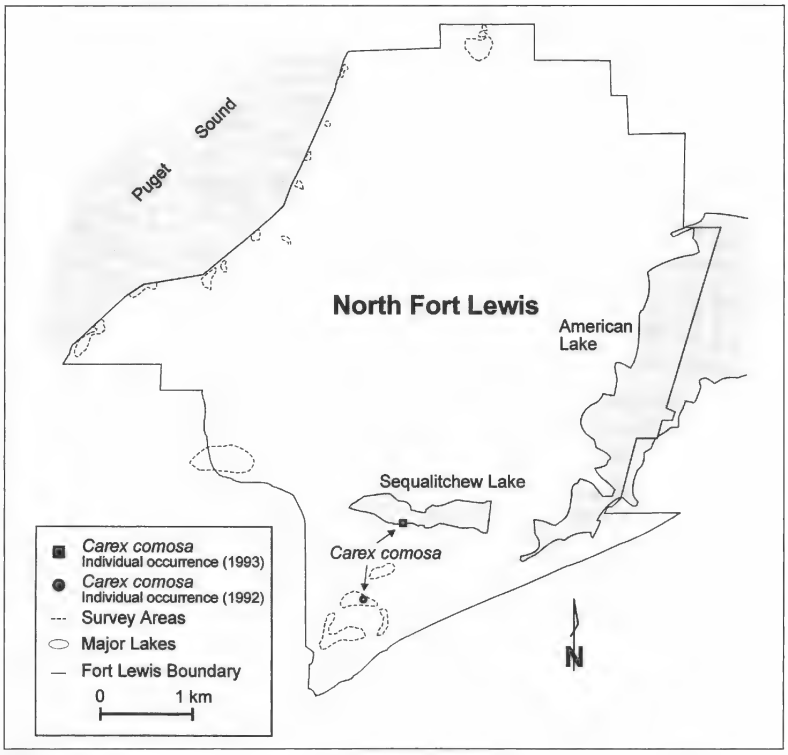

Figure 6. The locations of *Carex comosa* clumps on North Fort Lewis.

bracts atop the stem and a sessile, pearly white flower. The short (3-4 cm), upright petals are rounded at the tip and lanceolate in outline. Flowering season ranges from late March through mid May. Some plants bear mottled bracts, and immature specimens may possess only one or two bracts.

A regional endemic, *T. parviflorum* ranges from Pierce and Thurston Counties in Washington to northern Oregon (Soukup 1980). It is found in moist woodlands, often with a well-developed shrub understory. The species is classified as sensitive in Washington (WNHP 1994).

Habitat and associated species. We found *T. parviflorum* on sites dominated by shrubs with cover ranging from 25 to 95%. Tree cover ranged from 20 to 55% with the understory composed of moderate to high cover (50-70%) of forbs, grasses, and mosses (Table 4). The most common and abundant associated species were *Q. garryana*, *Fraxinus latifolia*, *Oemleria cerasiformis*, *Holodiscus discolor*, *Crataegus douglasii*, *Symphoricarpos albus*, *Pteridium aquilinum*, and mosses (*Kindbergia oregana*, *Rhytidiadelphus triquetrus*, *Hylacomium splendons*). Understory forbs included the non-native species *Hypericum perforatum*, *Solanum dulcamara*, and *Cirsium arvense*; and disturbance-adapted natives such as *Urtica dioica*.

Pattern of abundance. Although we found apparently extensive, suitable habitats at several survey locations, less than 10% were occupied by *T. parviflorum*. Single, scattered plants were found in some areas, and large populations (500-1000 individuals) were observed at two locations. In these areas, plants occurred singly or in compact clusters.

Topography and soils. Plants were found on flat to gently sloping ground adjacent to lakes and streams. Substrate at all observed *T. parviflorum* sites consisted of leaf litter (1-3 cm deep) and a layer of dark, moist organic soil (5-25 cm deep) atop gravelly, glacial outwash.

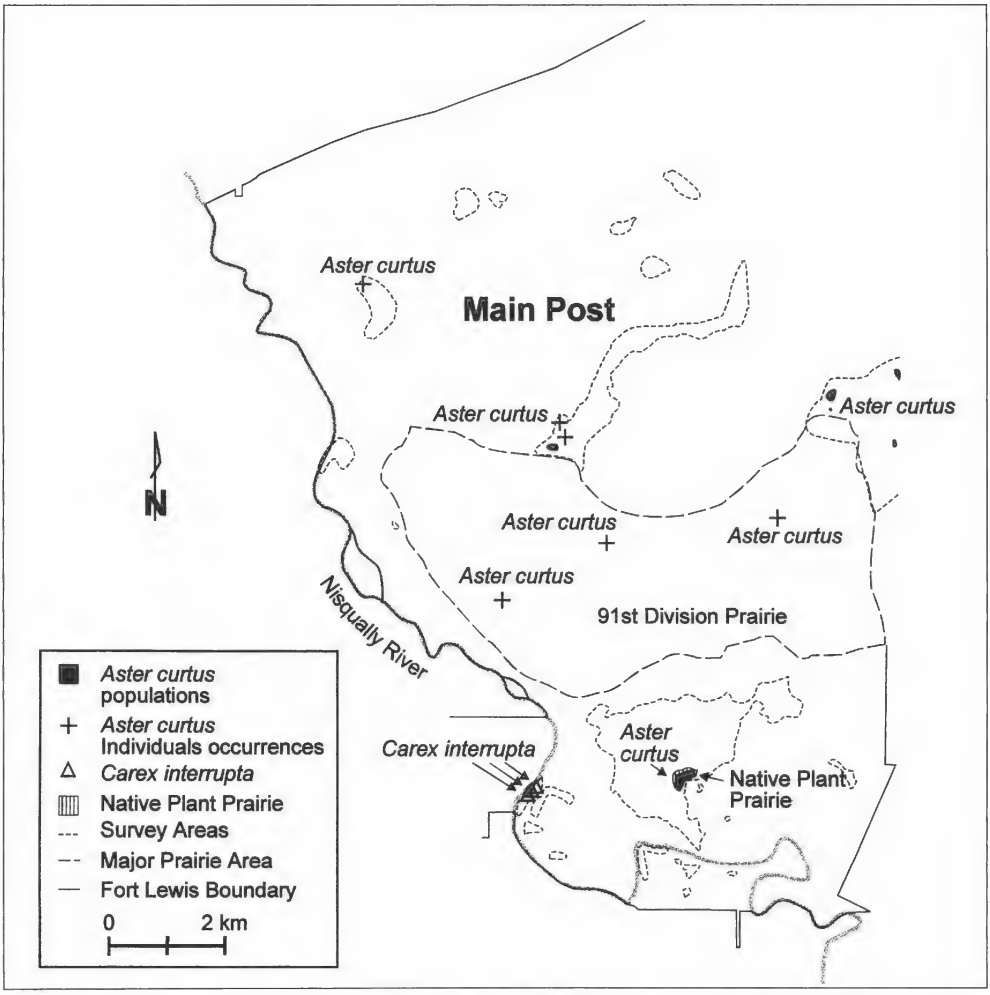

Figure 7. The location of *Carex interrupta* individuals and *Aster curtus* populations on the main post, Fort Lewis.

Phenology. We found flowering plants in all populations, with an average of 60% flowering and 40% in the vegetative stage. All age classes, from juveniles with one or two bracts to robust, flowering adults, were represented at sites with large populations (over 50 plants), but some populations were composed of very few, widely scattered individuals.

Carex comosa

Species description. Carex comosa is a perennial wetland plant that produces dense clusters of stems from a short, stout rhizome. Individual plants occur in clumps, rooted in wet soils or on hassocks of other sedges (WNHP Information System). With coarse, bright-green blades, 5 to 10 dm tall, and prominent, cylindrical pistillate spikes on slender, nodding peduncles, this species can be distinguished from common, associated sedges at a glance. The perigynia also are distinctive—green when young, becoming reddish or straw colored at maturity, and prominently beaked with arching, divergent teeth (Hitchcock et al. 1969). Flowers and fruits are produced from late May through August.

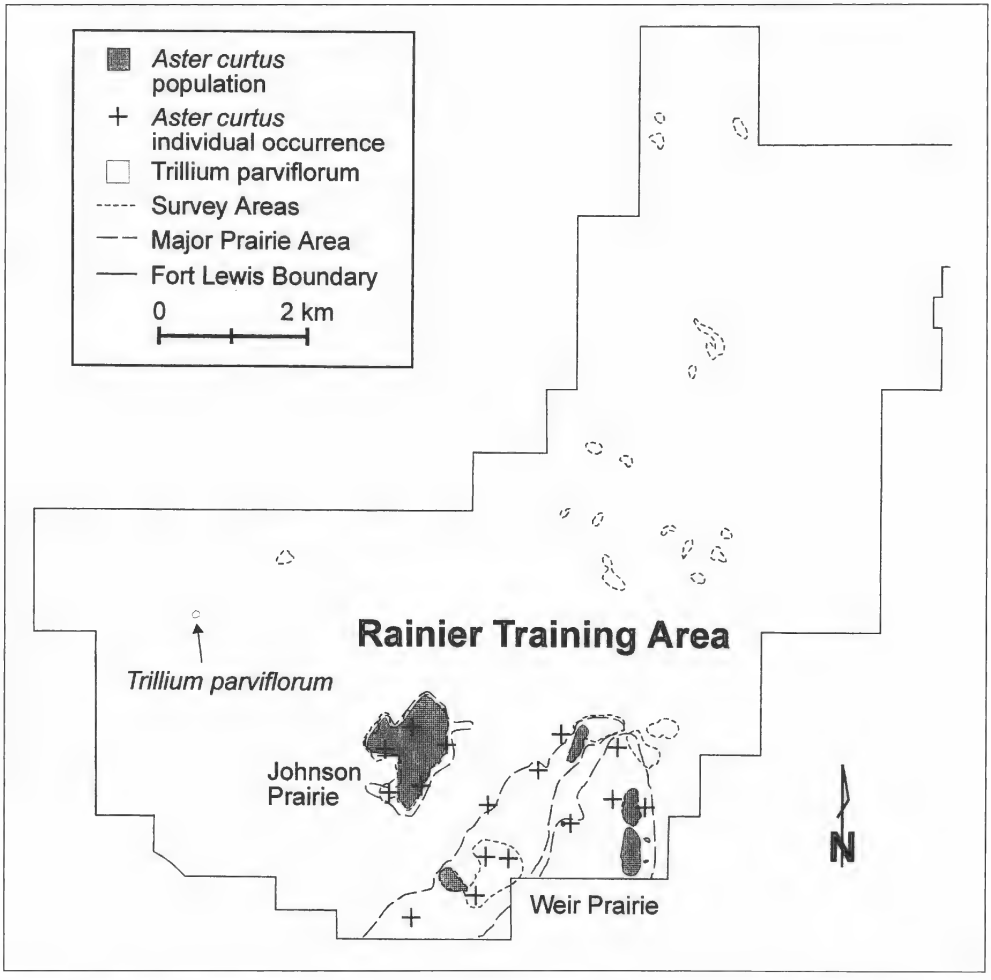

Figure 8. The location of *Aster curtus* and *Trillium parviflorum* populations on the Rainier training area, Fort Lewis.

Carex comosa ranges from Québec southward to Florida and Louisiana, with scattered, disjunct populations in Washington, Oregon, California, and northern Idaho (Hitchcock et al. 1969). Although somewhat common east of the Rocky Mountains, it is rare in western states and is listed as sensitive in Washington (WNHP 1994). Confirmed *C. comosa* sites in Washington State include swamps, lake margins, and ditches (WNHP Information System).

Habitat and associated species. We found one population of *C. comosa* in a freshwater marsh (MacKay Marsh) in June 1992. We found a second population on the south shore of Sequalitchew Lake in August 1993. *Carex comosa* occurred in open areas dominated by wetland forbs and graminoids (cover ranged from 15 to 60%) with minor woody cover (15%) and some standing water (25%, Table 5). Dense shrub communities (over 70% cover) occurred along the margin of MacKay Marsh. *Carex comosa* was not found in these shrub-dominated areas.

Many native plant species not commonly found in Fort Lewis wetlands occurred with *C. comosa* at MacKay Marsh. We sampled 24 wetlands and found 6 species that were exclusive to MacKay

TABLE 2. Native species commonly associated with *Aster curtus* on native-dominated prairies and prairie-forest mosaic plant communities. Average cover and frequency was determined on Fort Lewis prairies that met the criteria for native-dominated plant communities, i.e., >50% cover native species and >10% *Festuca idahoensis*.

Native species	Cover (%)	Frequency (%)
Festuca idahoensis	37	75
Aster curtus	2.9	36
Erigeron speciosus var. *speciosus*	5.7	9
Poa compressa	4.1	32
Carex pennsylvanica	2.7	21
Pteridium aquilinum	2.5	20
Symphoricarpos albus	2.8	13
Lupinus bicolor	2	10
Quercus garryana	2	10
Pseudotsuga menziesii	2	26
Lupinus lepidis	1	40
Eriophyllum lanatum	1	56
Lomatium utriculatum	1	36
Lupinus albicaulis	1	31
Zigadenus venenosus	1	18
Campanula rotundifolia	1	28
Danthonia californica	1	50
Fragaria virginiana var. *platypetala*	1	27
Panicum scribnerianum	1	21
Luzula campestris var. *multiflora*	1	31
Camassia quamash	0.5	37
Viola howellii	0.5	13
Viola adunca	0.5	07
Koeleria acrantha	0.5	16
Spiranthes romanzoffiana	0.8	06
Mosses		
Racomitrium canescens	6	51
Polytrichum juniperum	3.6	36
Lichen		
Peltigera canina	1	10
Litter	4.3	30
Bare ground	7	36

TABLE 3. Non-native species and common native species associated with *Aster curtus* on alien-dominated prairies and prairie-forest mosaic plant communities.

Species	Cover (%)	Frequency (%)
Agrostis tenuis	31	85
Hypochaeris radicata	9	79
Plantago lanceolata	5	57
Cytisus scoparius	4.7	28
Leucathemum vulgare	4	23
Cytisus scoparius (dead, burned in 1993)	3.8	21
Vicia sativa	3.8	17
Trifolium procumbrens	3	54
Poa pratensis	3.2	41
Trifolium pratense	29	36
Holcus lanatus	2.2	61
Anthoxanthum odoratum	1.8	13
Aster curtus	1.6	14
Agropyron repens	1.4	17
Bromus mollis	1	28
Aira praecox	1	48
Hypericum perforatum	1	66
Dactylis glomerata	1	29
Rumex acetosella	0.5	28
Aira caryophylla	0.5	36
Teesdalia nudicaulis	0.5	40
Mosses		
Racomitrium canescens	4.9	43
Polytrichum juniperum	3	47
Lichen		
Peltigera canina	1	10
Litter	7	54
Bare Ground	5	45

Marsh and are generally characteristic of bogs: *Scutellaria galericulata*, *S. lateriflora*, *Hydrocotyle ranunculoides*, *Ledum groenlandicum*, *Drosera rotundifolia*, and *Vaccinium oxycoccos*. The following typical wetland species were present: *Potentilla palustris*, *Juncus balticus*, *J. articulatus*, *J. acuminatus*, *J. tenuis*, *Typha latifolia*, *Sparganium emersum*, *Mimulus guttatus*, *Spirea douglasii*, and *Salix sitchensis*. *Salix lasiandra*, *S. geyeriana*, and *Betula glandulosa* also were present along the margin of MacKay Marsh. *Phalaris arundinacea*, an aggressive, alien wetland plant, covered about 30% of this marsh and is likely to increase if allowed to persist (Hutchinson 1992).

The *C. comosa* populations (20 individuals) found at Lake Sequalitchew covered about 5% of a patch of native-dominated wetlands with an assortment of alien species in trace amounts. *Salix sitchensis*, *S. piperi*, *Alnus rubra*, *Potentilla palustris*, *J. tenuis*, *J. acuminatus*, *J. articulatus* and a moss, *Philonotis* sp., covered >70% of the area. *Phalaris arundinacea* cover was 15%, and several other alien species were present.

TABLE 4. Common plants associated with *Trillium parviflorum*. Plant species are listed by rank of their average % cover for each vegetation stratum. Site and species information was collected from 11 sites harboring *Trillium parviflorum*.

Species	Cover (%)	Frequency (%)
Trees		
Quercus garryana	35	55
Pseudotsuga menziesii	35	55
Fraxinus latifolia	19	27
Shrubs		
Symphoricarpos albus	49	55
Acer circinatum	24	18
Oemleria cerasiformis	20	73
Holodiscus discolor	10	9
Berberis aquifolium	2	18
Rubus procerus	4	18
Rubus ursinus	1	9
Forbs/Graminoids		
Trillium parviflorum	12	100
Galium aparine	3	55
Montia sibirica	3	45
Solanum nigra	3	18
Tellima grandiflora	2	27
Nemophila parviflora	1	45
Circaea alpina	2	18
Osmorhiza chilensis	2	18
Bromus vulgaris	1	18
Leucanthemum vulgare	1	18
Dactylis glomerata	1	18
Hyphochaeris radicata	0.5	27
Lactuca muralis	0.5	18
Arctium minus	0.5	18
Moss/Lichen		
Kindbergia oregana	25	55
Rhytidiadelphus triquetrus	5	27
Isothecium stoloniferum	4	18
Plagiomnium sp.	2	9

TABLE 5. Common plants associated with *Carex comosa*. Plant species are listed by rank of % cover, based on their occurrence at MacKay Marsh and Lake Sequalitchew. Native plants dominated the locations; alien plants are also listed.

Species	Cover (%)
Salix lasiandra	20
Salix sitchensis	20
Salix piperi	10
Salix geyeriana	8
Phalaris arundinacea	8
Spiraea douglasii	6
Potentilla palustris	5
Typha latifolia	3
Kalmia microphylla	2
Agrostis tenuis	1
Mimulus guttatus	1
*Ledum groenlandicum**	1
*Vaccinium oxycoccos**	0.5
*Drosera rotundifolia**	0.5
Juncus tenuis	0.5
Juncus acuminatus	0.5
Juncus articulatus	0.5
Juncus balticus	0.5
Eriophorum chamissonis	0.5
Cytisus scoparius	0.5
*Scutellaria galericulata**	0.5
*Scutellaria lateriflora**	0.5
*Hydrocotyle ranunculoides**	0.5
Sparganium emersum	0.5
Mosses	
Philonotis spp.	10
Spaghnum capillifolium	3
Spaghnum palustre	0.5
Spaghnum squarosum	0.5

* Species that were exclusive to MacKay Marsh.

Pattern of abundance. *Carex comosa* covered less than 1% of the MacKay Marsh location. The population consisted of six clumps (one clump equals an individual) distributed over an area of ca 1000 m^2. Distance between individual plants ranged from 5 to 100 m.

Topography and soils. Three of the six plants were found in standing water (5-20 cm deep) at time of initial survey at MacKay Marsh (2 June 1992). All clumps were found in open areas without shade from forbs or woody plants. The substrate consisted of fine silt (10-20 cm) over gravel at MacKay Marsh. The substrate at the Sequalitchew Lake site consisted of sandy loam soils over gravel outwash.

Phenology. All the plants we observed bore fruit and appeared robust (there was no evidence of herbivory or senescence). No seedlings or immature clumps were found. Additional plants may exist, but we were unable to access interior portions of this swamp by foot or canoe. At Sequalitchew Lake, about 85% of the plants were in fruit with the remaining being in the vegetative stage.

Carex interrupta

Species description. Carex interrupta is a rhizomatous, perennial plant that forms loose clumps of stems 1.5 -7 dm tall. Flowering stalks bear 2-7 erect, slender pistillate spikes and a terminal staminate spike. The olive-green perigynia are very small, each subtended by a purplish black pistillate scale (Hitchcock et al. 1969). Plants generally produce flowers and fruits from April through July. Precise measurement and observation of the perigynia and mature achenes is necessary to distinguish *C. interrupta* from closely related species with overlapping range.

Carex interrupta favors sandy or gravelly river banks, streambeds, and open, wet areas at low to moderate elevations. Reported from areas scattered throughout Washington, the species also ranges southward into Oregon, where it can be found west of the Cascade Range (Hitchcock et al.1969). *Carex interrupta* is classified as a monitor species in Washington (WNHP 1994). It currently is considered to be more abundant and less threatened in Washington than was previously assumed.

Habitat and associated species. We found one confirmed population of *C. interrupta* along the Nisqually River. *Carex interrupta* clumps were on sparsely vegetated, sandy banks on a gravel river bar. Forbs and graminoids comprised the dominant vegetation (35 % cover), with minor cover (5%) in the woody species, *Salix sitchensis* and *A. rubra*. Associated species include *J. ensifolius*, *Mimulus guttatus*, *Scirpus microcarpus*, *Carex* spp., *Epilobium* spp., and *Veronica* spp. Alien plants such as *Melilotus officinalis*, *Phalaris arundinacea*, and *Ranunculus repens* also were present.

Pattern of abundance. About 20 clumps (each clump comprising an individual) occurred along a 100-m section of the north bank. *Carex interrupta* occupied about 5% of the 500 m^2 area, but visual estimates of cover for this species were difficult because it intermingled with *C. sitchensis* in this location, and the vegetative portions of these species are indistinguishable.

Topography and soils. The bank slope was gentle (slope <5%), and no evidence of slope instability was observed at the site. Dry, waterborne debris was observed on the upper banks, above the *C. interrupta* clumps, which indicated that the population was submerged during high water events. Soils were composed of bare sand and a thin layer (1 cm) of organic material over sorted gravels and cobbles.

Phenology. Mature reproductive structures are required for positive identification, hence all confirmed *C. interrupta* specimens bore fruit. Among all *C. interrupta*-like sedge clumps observed at the site, 80% bore fruits, 10% had shed all seeds by survey date (9 July 1992), and 10% exhibited only vegetative growth.

Threats to rare species populations at Fort Lewis

Several threats were apparent to each of the rare species present at Fort Lewis. The threats to each species and some recommendations for species conservation are discussed below.

Aster curtus

Loss of suitable habitat and reduction in plant populations due to the successional advancement of *P. menziesii*, encroachment by non-native species such as *Cytisus scoparius*, and physical disturbance (overland vehicular traffic and military training activities) are the greatest threats at FLMR.

Fort Lewis initiated efforts to protect *A. curtus* populations in 1987. This program includes removing of *P. menziesii* , burning *C. scoparius* to maintain prairie plant communities, and prohibiting physical damage to *A. curtus* sites by posting signs to keep vehicles out of areas having large populations.

Surveys of *A. curtus* conducted in 1984 (Sheehan and Clampitt) and 1991 (Gilbert et al.) indicated significant changes in species richness and vegetative cover at permanently marked monitoring plots, but no significant change in the abundance of *A. curtus*. Even though Gilbert et al. (1991) concluded that current management activities to preserve *A. curtus* on FLMR are effective, additional research and monitoring efforts would augment assessing the long-term effectiveness of management plans.

Aster curtus is well suited to long-term demographic study at FLMR because the population is large, and substantial numbers of plants are found in a range of habitat conditions, from somewhat pristine to degraded. Of all rare plants extant at FLMR, *A. curtus* inhabits the most accessible natural areas (open prairies with good road access) and the habitat most likely to be transformed

by plant succession and weed invasion. Susceptible to physical destruction and displacement by competitor species, the *A. curtus* population at FLMR merits continued monitoring.

Trillium parviflorum

Based on field observations in 1992 and 1993, threats to *T. parviflorum* populations at FLMR appear to be minor at this time. Threats include competition with associated species, both native and non-native. There was uncertain reproductive success at sites with few, scattered individuals. Monitoring some of the populations to detect changes in the population numbers and vigor of the plants may provide evidence for a continued need for monitoring in permanent plots. Several individuals of *T. parviflorum* showed signs of seed predation; Kruckeberg (1991) observed ants eating the seeds of the *T. ovatum*. Additional work will be required to accurately assess the conservation needs for *T. parviflorum*.

Carex comosa

The environmental circumstances under which the current population of *C. comosa* developed are unclear, and no demographic information is available to indicate growth rate of the population. Specific threats are difficult to infer from a single visit to a population of six individuals, but observations from the 1992 survey do suggest factors that may influence the continued persistence of *C. comosa* at Fort Lewis.

The presence of water control structures (a head gate and human-made outlet channel at MacKay Marsh) and the abundance of reed canary grass show that the swamp is not pristine. Aerial photographs from 1981 show little open water in MacKay Marsh and no visible snags. In 1992, we encountered large areas of open water and numerous standing dead *Populus trichocarpa*, *Pinus contorta* var. *contorta*, and *Pyrus fusca* on the margins and in MacKay Marsh. Water level and woody-plant cover have fluctuated during the past decade. *Carex comosa* was not found on sites with dense cover of shrubs and trees, but woody vegetation dominates the surrounding area and may spread into the habitat of this rare species. The impact of changes in water level and woody cover on *C. comosa* should be examined.

No seedlings or small plants of *C. comosa* were found, indicating a lack of seedling reproduction under the current environmental and physiological conditions. Vegetative reproduction was not apparent for this population. The total number of reproductive adults is small and individual plants are widely scattered. Therefore, such a population may possess low genetic diversity and concomitant inability to adapt as environmental conditions change (Owen and Rosentreter 1992). Such small populations are especially susceptible to stochastic effects, including environmental disturbance (fire, drought) and chance death of numerous individuals.

Carex interrupta

Based on initial observation of *C. interrupta* at FLMR, competition from native and non-native species may be a threat. Abundant bare ground on the gravel bar of the Nisqually River is available for colonization by native and alien species, and loss of individual clumps of *C. interrupta* may be displaced by other species or physically during high-water events. Minor herbivory was observed; bracts were partially eaten from two *C. interrupta* clumps.

Management Recommendations

Each ETS plant species occurring at FLMR is restricted in its distribution by the interactions of its unique population dynamics and environmental conditions it finds favorable. No single management practice can provide the requirements for all four species. A basic monitoring protocol, tailored to each species, would provide information necessary to evaluate the efficacy of management, however. The conservation strategies, monitoring, and research endeavors summarized below are designed to protect extant populations and provide information to assess long-term viability of these populations. Because our knowledge of the species and the efficacy of the management techniques is rudimentary, management must be adaptive, incorporating monitoring and feedback to redirect management activities. Before beginning such programs however, the land manager must decide what time, funds, and personnel will be allocated to the maintenance and monitoring of ETS plant species (Owen and Rosentreter 1992) and develop management plans accordingly.

(1) *Protection.* Protect extant populations from physical damage from rubber-tired or tracked vehicles. Establish biodiversity preserves to pro-

tect and manage ETS plant populations and habitat. Emphasis should be placed on improving and maintaining critical wetland and prairie communities that contain the ETS species, high percentages of native species, and little or no evidence of disturbance from non-native species, military training maneuvers, historic grazing, or cultivation.

(2) *Rehabilitation of degraded habitat.* Control the spread of competing and non-native species or actively remove non-native species. Erosion control, maintenance of stream crossings, and maintenance of water levels in wetlands are measures that would improve the habitat of ETS species and native plant communities.

(3) *Monitoring.* Periodically review results of management plans, including the effects on plant demography and habitat quality to see if the plan is adequate or if it needs revision (Pickart 1991). Record habitat information (distribution and abundance of associated species, cover types, physical characteristics of site) and life stage, flowering, seed production, and dispersal of individuals (Dixon and Cook 1989; Menges 1990; Pickart 1991).

(4) *Propagation.* If populations decline, a program of germination or vegetative propagation, revegetation, and habitat restoration could be considered.

Research in conjunction with monitoring of management efficacy could provide additional information on the life history and habitat of ETS plants and factors limiting their populations. Additional research, experimental or retrospective, could quantify the demography of plant populations in relation to degree of disruption or manipulation that alters habitat. Genetic material from plants within and among patches throughout the FLMR could be analyzed to determine the amount of variation within FLMR populations. Because lack of genetic variation can inhibit a population's ability to respond to environmental changes, such information should be considered when developing long-term management plans for ETS species (Owen and Rosentreter 1992). Research on the reproductive capability of ETS plant species is needed. Seeds could be collected, germinated, and grown under controlled conditions that simulate natural phenomena (i.e., test effect of freezing, long-term storage, or inundation of water on seed viability) (Dixon and Cook 1989).

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Statistical Relationships between Topography and Precipitation in a Mountainous Area

Abstract

This study contributes to a goal of the Mackenzie GEWEX (Global Energy and Water Cycle Experiment) Study to model the water and energy balances of the Canadian Arctic Basin on spatial scales of 100 kilometres and time scales of one month. Accurate estimates of the spatial distribution of precipitation at these scales are critically important inputs into hydrologic models used to simulate these processes over complex terrain. The development of a suitable precipitation model for the Mackenzie basin is seen as an important step in our understanding of climate variability and climate change under conditions of increasing concentrations of atmospheric greenhouse gases. In this study, univariate linear regression is employed to determine the relationships between monthly precipitation and orographic parameters including elevation, aspect and slope in the mountainous terrain of Williston Basin located in north central British Columbia. Slopes, aspects and elevations are calculated using a 5-minute digital elevation model (DEM). The study finds several statistically significant ($p<.05$) correlations between elevation and monthly precipitation for terrain having either north or east aspect based on individual Julys between 1986 and 1990. Terrain having south or west aspect displays very low correlations for those same months. For winter conditions, the relationship between precipitation and elevation is generally weak for all aspects for individual Januarys between 1986 and 1990. The lack of correlation with wintertime precipitation may very well be due to the poor quality data related to snow undercatch which is estimated to be roughly 50 percent. The quality and quantity of the data generally is also suspect owing to the volume of missing records and the short period of record. Station elevations and DEM elevations correlate equally well with monthly precipitation, contrary to the findings of several recent studies which show better correlations using coarser resolution. The study found no consistent relationship between monthly precipitation and slope in summer or winter.

Introduction

This study was undertaken under the umbrella of the Global Energy and Water Cycle Experiment (GEWEX) project, the Canadian portion of which is referred to as the Mackenzie GEWEX Study (MAGS). A goal of GEWEX is to model the water and energy balances of the Canadian Arctic Basin on spatial scales of 100 kilometres and time scales of one month. The overall aim of this study was to model the effects of orographic enhancement on the spatial distribution of precipitation in mountainous terrain. The Williston basin was chosen because of the existence of a relatively dense hydrometeorological network operated by British Columbia Hydro. The approach was to determine statistical relationships in an area of rugged terrain which was well represented by climate data. The ultimate goal is to apply these relationships to more data-sparse regions of the Mackenzie basin. The development of a suitable precipitation model for the Mackenzie basin is seen as an important step in our understanding of climate variability and climate change under conditions of increasing concentrations of atmospheric greenhouse gases.

The objectives of this study were to determine the elevation, slope, aspect and exposure to southwesterly winds for 28 B.C. Hydro climate stations in the watershed; to develop and test statistical relationships between these orographic parameters and monthly or seasonal precipitation; and use these relationships to determine the average variance in precipitation that can be attributed to each of the orographic parameters.

A previous study of the Williston basin by Environment Canada (B. F. Findlay personal communication) showed only a weak relationship between monthly precipitation and elevation. The study cited gauge siting in narrow valleys oriented obliquely to the prevailing winds as a major reason for the weak statistical relationship. The study also advised caution in the use of B.C. Hydro data based on comparisons with Environment Canada principal station data within the same geographic region.

The first phase of the present study was to focus on statistical relationships between monthly and seasonal precipitation and the various orographic parameters. The second phase will be to develop a model based on these statistical

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relationships and to apply the model to a mesoscale grid of the Williston Basin. The third and final phase of the project will apply the model to the more data-sparse regions of the Mackenzie basin. The purpose of this paper is to summarize the findings of the first phase of the project.

Background

The Williston Basin, including the region immediately to the east of the Rockies covers an area of more than six million hectares. The study area shown in Figure 1 is centered at roughly 56 degrees North and 124 degrees West in north-central British Columbia. The main body of Williston Lake is a prominent feature of the basin having a northwest-southeast orientation and lying in the Rocky Mountain Trench. The elevation of the lake is roughly 680 metres, and it is bordered on either side by mountain ranges rising to more than 2000 metres. Another arm of Williston Lake branches eastward from the trench to the Bennett Dam which empties into the Peace River.

The region has a continental type of climate which is characterized by cold, dry winters and warm, somewhat wetter summers (Environment Canada, 1990). The Coast Mountains well to the west remove much of the moisture from the maritime air masses which eventually move across the province into the Williston Basin. The wettest season is the summer during which convective weather predominates. The winter and spring months become progressively drier with the driest months being February, March and April. The winter is characterized by frequent cold spells as dry, Arctic air forces its way southward and westward through the mountain passes from Alberta and the Northwest Territories. The prevailing flow at mid-atmospheric levels is generally from the west or southwest.

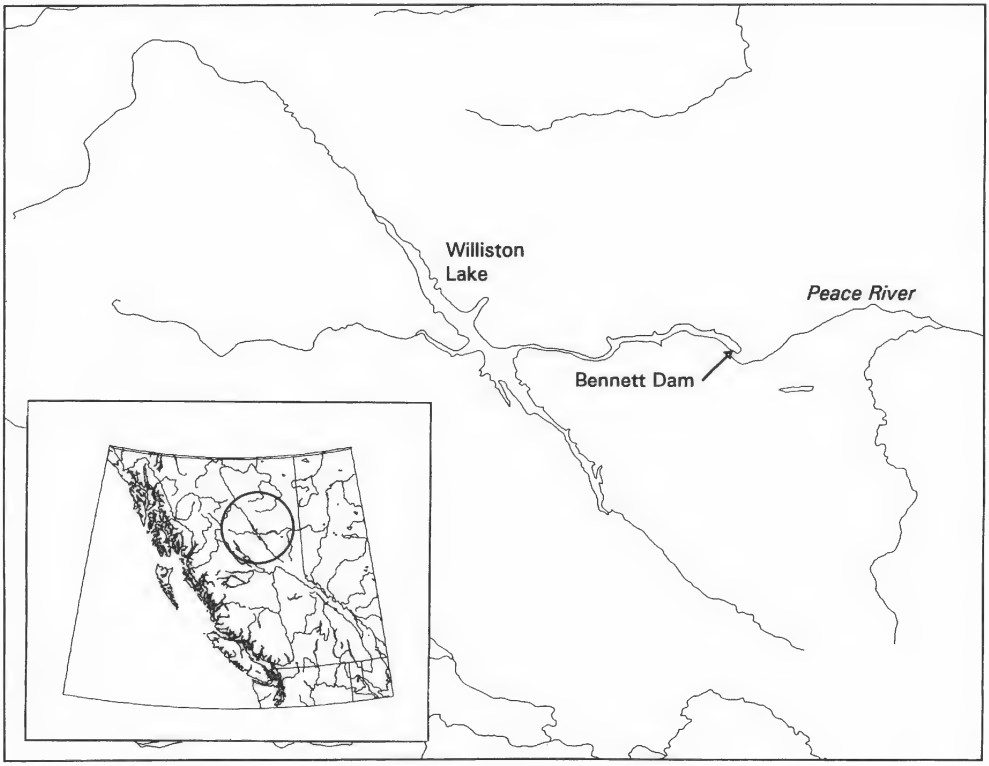

Figure 1. Map of Williston Basin. Inset: Map of British Columbia showing the study area.

Approaches to Estimating Precipitation in Mountainous Regions

The precipitation falling on a mountainous region may be thought of as having two components: an amount due to convergence which would occur in the absence of the mountains, and an orographic component which modifies these processes (Barry, 1981). The physical basis for orographic enhancement is that mountain barriers act on the flow of moist upper air in such a way as to deflect the airmass upward as it flows over the terrain, or to cause upward motion due to convergence in valleys. As this moist airmass rises it expands and cools thus enhancing condensation and the formation of precipitation. As a result, both the amount and the rate of precipitation are increased. Conversely, air subsiding down mountain slopes compresses and warms producing a drying effect in the lee of the mountains. Additionally, mountain barriers tend to retard the flow of air resulting in the modification of frontal systems in complex terrain. Mountains also promote local convection which produces showery summer weather (Bonacina, 1945).

The requirement for estimates of spatially distributed precipitation frequently arises in hydrologic modelling and in a variety of agricultural and natural resource applications. Generating these spatial distribution patterns usually involves interpolating from point station data to points on a grid for use in computer models. However, simple interpolation techniques fail to account for the effects of topography, which are a significant factor in the distribution and intensity of precipitation in mountainous terrain (Phillips et al., 1992). For example, it is well known that precipitation generally increases with elevation, and that the windward slopes of mountains typically receive much more precipitation than the leeward slopes. Thus, physical processes attributed to elevation, slope and aspect need to be included in any model if accurate estimates of the distribution of precipitation are to be obtained. To complicate matters, mountainous regions tend to be sparsely monitored by climate stations, and those stations that do exist tend to be sited at low elevations in valleys yielding little information about the relationship between topography and precipitation at higher terrain.

The need for interpolation techniques that account for the effects of topography on the distribution of precipitation in data-sparse mountainous regions has been the subject of much investigation. Daly et al. (1994) categorize approaches for estimating the spatial distribution of precipitation into three groups: graphical, topographical, and numerical. Graphical methods include isohyet mapping and Thiessen polygon estimation. The latter method utilizes the ratio of the zone of influence corresponding to each station to the total area of interest as a means of assigning weights to individual data points (Thiessen, 1911).

Topographical methods involve correlating point precipitation data with various topographical and meteorological parameters such as slope, elevation, aspect, orientation, and wind speed and direction. In a study conducted in western Colorado, Spreen (1947) found that about 85% of the variation in precipitation was accounted for by elevation, rise, exposure and orientation, while only 30% was attributable to elevation alone.

Numerical methods involve spatial interpolation techniques in which the data are weighted according to some function. For example, inverse distance weighting assigns weights to data inversely proportional to the distance between points. However, these distance weights are not necessarily optimal in producing the best estimate of precipitation. A class of methods for choosing interpolation weights so as to optimize the interpolation function is called optimal interpolation. Kriging is one type of optimal interpolation scheme whereby interpolation weights are obtained by fitting a semivariogram to the data (Burroughs, 1986). Tabios et al. (1985) systematically compared a variety of spatial interpolation techniques and found these so-called geostatistical methods such as kriging to be superior to other interpolation schemes including inverse distance weighting and Thiessen polygons.

As Daly et al. (1994) point out, the application of geostatistical techniques is limited to areas characterized by a single orographic regime which maintains a strong overall elevation-precipitation relationship. Such homogeneity is typically limited to relatively small areas of complex terrain. The relationship between elevation and precipitation, for example, over large, non-homogeneous regions may in fact be inverse. Such is the case when considering the region between the wet, coastal areas of British Columbia and the

higher, but drier, interior plateau regions (Basist et al., 1994).

A relatively new model known as PRISM, an acronym for Precipitation-elevation Regressions on Independent Slopes Model (Daly et al., 1994), combines physical and statistical approaches to the analysis of orographically enhanced precipitation. The PRISM model is based on the observation that relatively coarse scale "orographic" elevations are more highly correlated to precipitation than are point station elevations (Chuan and Lockwood, 1974). Accordingly, the model substitutes station elevations with digital elevation model (DEM) elevations using 5-minute latitude/longitude grid spacing. Each grid cell has an elevation and slope orientation (aspect) computed from the elevation gradients. Grid cells are then grouped into topographic facets according to the direction of their slope orientation (i.e. north, east, south, west).

In an evaluation of the model, PRISM was applied to the Willamette River basin in Oregon, allowing a direct comparison of model performance to the results obtained by Phillips et al. (1992) who used kriging, elevation-detrended kriging, and cokriging. In that region, PRISM performed better than any of the other methods as measured in terms of cross-validation errors. The PRISM model was also successfully applied to larger geographic areas including northern Oregon as well as the entire western United States with only slight deterioration in statistical performance. The superiority of PRISM lies in its ability to continuously adjust its frame of reference by using local precipitation-DEM elevation relationships.

The PRISM model may be compared to the "square grid technique" (Solomon et al., 1968) which was recently applied to the Mackenzie basin as part of the Mackenzie Basin Impact Study to model changes to runoff under different climate change scenarios (Soulis et al., 1994). Like PRISM, this technique also utilizes a 5-minute DEM and derives other physical characteristics such as slope and aspect for each grid cell from the elevation data. Multiple regression is then performed using these data on temperature, precipitation and evaporation which are then used as inputs to a runoff model.

In the original study in 1968, the square grid technique was applied to Newfoundland, and its accuracy was verified against measured precipitation. The island of Newfoundland has an area of 110 thousand square kilometres, and the investigators divided the island into two regions, an Eastern Region and a Western Region, each with its own unique precipitation regime. A unique multiple regression equation was found for each region. This procedure is also consistent with the premise of PRISM which considers only slopes which lie on topographic facets representing homogeneous orographic precipitation regimes.

The main difference between PRISM and the square grid technique is that PRISM is based solely on the relationship between elevation and precipitation within defined orographic regimes. The square grid technique, on the other hand, includes several independent variables such as distance from the sea, barrier heights, a latitude index, and the average slope of the grid square, from which multiple regression equations are derived with respect to precipitation.

Methodology

Precipitation data from B.C. Hydro's hydrometeorological network were obtained organized and verified. A terrain analysis was then performed using gridded DEM elevation data to obtain elevation, slope and aspect for each grid cell. Finally, a statistical analysis was undertaken to look for significant correlations between monthly and seasonal precipitation data and the orographic parameters. Each of these procedures will be discussed in turn.

Precipitation Data

The climate data for the study were provided by B.C. Hydro which operates a hydrometeorological network of 28 stations consisting of 18 stations upstream of the Bennett Dam in the Williston Basin and another 10 to the east of the Rocky Mountains (Figure 2; Table 1).

The network was created in 1980 with the installation of nine stations. Several more went into service between 1981 and 1983, and by 1984, 25 stations were operational. The last three were added between 1985 and 1988. The network was still in operation as of October, 1995, although data for this study were obtained for only up to 1992.

The precipitation data consist of hourly observations using Belfort automatic weighing-type

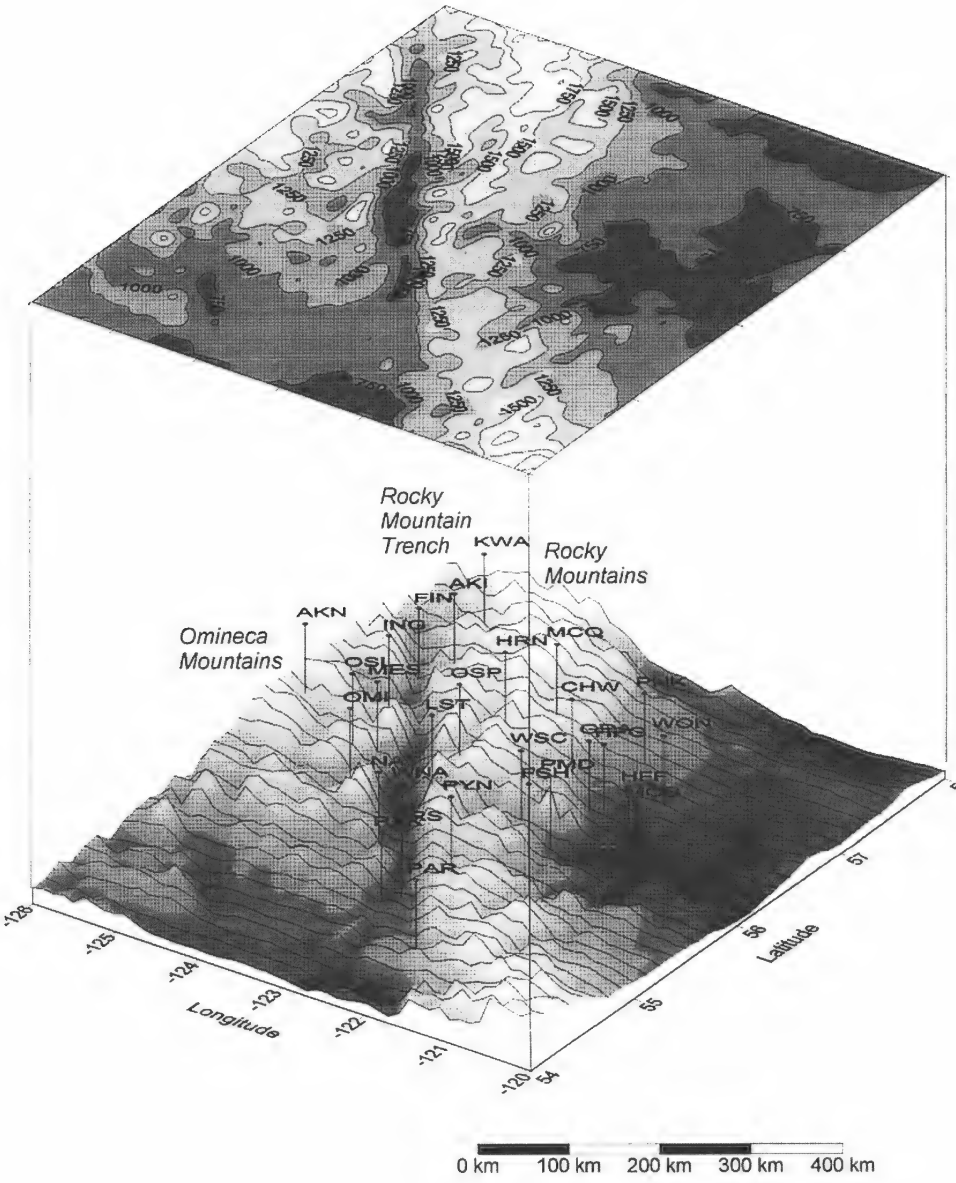

Figure 2. Topographic map of Williston Basin indicating the locations of BC Hydro hydrometeorological stations. The Rocky Mountain Trench, oriented southeast-northwest, separates the Omineca and Rocky Mountain ranges. Overlay shows elevation contours.

TABLE 1. List of stations within BC Hydro's Williston Basin hydrometeorological network indicating station identifiers, station elevations, DEM elevations, aspect and slope.

Station id	Station Name	Station Elevation (m)	DEM Elevation (m)	Aspect	Slope (m/km)
AKN	Aiken Lake	970	1385	W	34
AKI	Akie River	760	1320	W	40
CHW	Chowade Upper	1480	1228	N	34
FIN	Finlay above Akie	710	873	E	28
FSH	Fisher	750	972	N	13
PMD	GMS Hudson Hope	720	803	E	33
GRA	Graham River	700	812	N	9
HFF	Halfway River near Farrel Creek	480	635	S	3
HFG	Halfway River near Graham River	650	792	S	4
HRN	Horn Creek	1450	1561	E	21
ING	Ingenika River	700	895	S	2
KWA	Kwadacha River North	1554	1309	S	11
MCQ	McQue Terrace	1200	1481	N	2
MES	Mesilinka River	715	1199	E	55
MOB	Moberly River	600	659	N	5
NAT	Nation River	725	909	E	30
OMI	Omineca River above Osilinka	715	1029	W	35
OSL	Osilinka River	775	1235	W	17
OSP	Ospika River	750	1045	E	42
PAK	Pack River	675	775	N	4
PAR	Parsnip River Upper	790	895	S	17
PRS	Parsnip River above Misinchinka	700	852	N	16
PYN	Pine Pass	1400	1249	S	7
PNK	Pink Mountain	1204	1012	E	7
LST	Williston Lake at Lost Cabin	690	1006	W	28
WNA	Williston Lake at Nation Arm	680	748	E	10
WSC	Willison Lake nar Schooler	680	925	S	21
WON	Wonowon	910	842	S	3

precipitation gauges, and data are transmitted via satellite by means of data collection platforms. The contents of the gauge are weighed by means of a spring potentiometer. These gauges are reported to be accurate to 0.6 mm and the accuracy is temperature dependent (B.C. Hydro, 1994). A thin film of oil floats on the surface of the water in the container to prevent evaporation. During the winter, propylene glycol is added to the container to inhibit freezing. Some of the precipitation gauges at the 28 stations are shielded by means of an Alter shield which consists of a circular array of pickets surrounding the gauge to deflect the wind. A very limited amount of snow pack data is also available; three stations (Aiken Lake, Kwadacha River North, and Parsnip River Upper) are equipped with snow pillows which provide daily snow water equivalent measurements during the winter. Temperature data are also collected at each station. Servicing, which was performed four times per year in the past, has been recently reduced to three times per year. Beginning in 1991, B.C. Hydro began changing its entire network to standpipe gauges which are larger in diameter and have a greater holding capacity. However, most of the data used in this study were obtained from Belfort gauges.

Data from the hydrometeorological network are routinely quality controlled by B.C. Hydro and codes are manually assigned to each hourly observation as "good", "accumulated", or "missing". Accumulated precipitation amounts are obtained by recording the contents of the gauge following a period of time when either the instrument failed or when there were data transmission prob-

lems. Missing data are coded as such when no accumulated amount is obtainable. For example, when the gauge is filled to capacity, subsequent precipitation is coded as missing until the station is serviced.

Daily totals are obtained simply by aggregating hourly data, and the quality of the daily data is coded according to the poorest hourly observation during that day. For instance, if one hour of data is missing on a given day, then the daily total is coded as missing even though the other 23 hours may consist of good data. Approximately 20 percent of all daily hydrometeorological data are coded as either missing or accumulated.

The accuracy of snowfall measurements is problematic generally. The WMO, for instance, conducted an extensive study which concluded that snow in Scandinavia is underreported by automatic stations by about 50% (George Taylor, personal communication). A significant undercatch may result from blowing snow which is not detected by the gauge during windy conditions. The use of an Alter shield at some B.C. Hydro sites reduces the effects of wind but does not completely eliminate them. Also, only those sites which are highly exposed are shielded, so many of B.C. Hydro's gauges do not have shields.

Another problem that leads to underestimation of snowfall at B.C. Hydro sites is snow capping (Eric Weiss, personal communication). This occurs when the instrument is completely capped over with thick wet snow such that subsequent snow accumulations do not fall into the bucket and are not recorded by the gauge. This condition is most frequent when the temperature is near freezing and the snow is heavy and wet. Freezing can occur at sufficiently low temperatures when the glycol mixture becomes diluted as a result of the bucket being near capacity. Additional accumulations are not recorded once the mixture becomes frozen.

To assess the extent of the problem of underreporting of snow at B.C. Hydro stations, use was made of snow pillow data from one of the three stations, Aiken Lake, where such data is collected. An examination of the data shows a steady increase in the snow pack from about November through March each year, after which warm spring temperatures begin to melt the snow pack and values then decline. Using this fall-winter period of rising snow pack values, monthly aggregates of daily precipitation were compared to the corresponding monthly increase in the snow pack. Assuming negligible snowmelt during this period of low temperatures, it was found that only about 40% of the snow falling on the pillow is being detected by the Belfort precipitation gauge.

As a further assessment of the quality of B.C. Hydro data, monthly precipitation amounts were compared to those obtained for the same period from five Environment Canada (AES) stations located within the basin. Since AES climate observations are taken by human observers and the data are rigorously quality controlled, these stations serve as ideal benchmarks for determining the accuracy of the B.C. Hydro data. Only B.C. Hydro data coded as good quality were used. Of the 28 B.C. Hydro stations, 24 were found to have correlation coefficients of $r>0.7$ with at least one AES station, indicating good agreement. However, a comparison of snowfall between pairs of neighbouring AES and B.C. Hydro stations corroborated previous evidence of underreporting of snow at the automatic stations.

An underlying assumption of this study is that a spatial analysis can only be valid if the same set of precipitation events are observed from a number different points. For example, it would not be valid to compare monthly averages at two stations using different years of data to compute these averages. This requires that all stations have identical periods of record. However, because of the volume of missing data and the unequal periods of record at these stations, there is necessarily a trade-off between the number of stations which can be included and the length of record needed to obtain overlapping data.

The problem of large gaps in the records of some stations combined with the gradual introduction of new stations are limiting factors in the amount of data available for use. Confidence in monthly averages is improved by increasing either the number of events or the number of observation points. When data are missing at a particular station for a given period, a choice must be made to either drop the station from the analysis or reduce the period of record to be included. The trade-off is that the longer the common period of record desired to compute monthly averages, the fewer stations there are for which an uninterrupted period of record exists. Conversely, the more stations one may want to include, the shorter the period of record these stations have in common.

To maximize both the length of record and the number of stations with exactly overlapping periods of record on a monthly or seasonal basis, the year with the largest number of stations with good data was found. Then, subsequent years were added while dropping stations along the way whose period of record no longer overlaps that of the remaining stations. For example, to obtain five years of common record for a given month by this process, the number of stations was reduced from the original 28 to between nine and 15 depending on the month. To obtain a seasonal average for the combined summer months of June, July and August, the number of stations with five years of common period of record was ten.

The method of sampling is very important in the study of orographic precipitation because precipitation varies substantially both spatially and temporally. Using only ten stations in order to get five years of overlapping summer data has the effect of substantially reducing the sample size such that the topography-precipitation relationship may be inadequately sampled. On the other hand, while using a single month or season of data maximizes the sample size, the precipitation data could hardly be considered representative of longer term averages due to the high temporal variability in precipitation.

The temporal scale over which the precipitation-elevation relationship is valid, as well as the minimum averaging period required, remains uncertain (Daly, 1994). For this study, short periods such as monthly totals and five-year monthly averages were chosen in order to maximize the sample size. However, no attempt was made to optimize the precipitation-elevation relationship by using different time scales.

Terrain Analysis

A number of topographic parameters have been used in a variety of studies to explore the relationship between topography and monthly, seasonal and annual precipitation. Most were mentioned in the previous section. For the purpose of this study, relationships between elevation, slope and aspect and monthly precipitation were examined. A digital elevation model (DEM) was used for ease of computation of various orographic parameters, and to explore the difference between orographic (DEM) elevations and station elevations in terms of the elevation-precipitation relationship. In addition, an analysis of upper level winds was included as a basis for explaining the physical processes behind apparent statistical relationships between orography and precipitation.

A five minute DEM called TerrainBase (National Geophysical Data Centre, 1995) was used, and the same procedure employed by PRISM to calculate orographic elevations and slope orientations was applied to this analysis (Daly, 1994). According to this procedure, the orographic elevation of a station was calculated based on the elevations of the cell within which the station lies as well as the four adjacent cells. Cell elevations were weighted according to the inverse distance of the station from the centre of each of the five cells. In addition, station elevations were also obtained from the B.C. Hydro records for inclusion in the analysis. All elevations are expressed in metres.

Determining the aspect, or slope orientation as it is referred to by PRISM, of a grid cell entailed calculating north-south and east-west elevation gradients from pairs of adjacent cells. Each cell was categorized as either flat, north, east, south or west according to the orientation of the maximum gradient. A cell was considered flat if its east-west and north-south gradients was less than 15 metres.

Slope was defined as rise over run where the rise for each grid cell was defined by the maximum of the east-west and north-south gradients. The run was defined as the centre to centre distance between adjacent grid cells, ie.10 minutes of latitude for north-south gradients and 10 minutes of longitude for east-west gradients. The units of slope are expressed in metres per kilometre.

Since terrain features such as aspect and orientation have meaning only in relation to the wind direction, an analysis of 700 millibar winds was undertaken to establish the prevailing wind direction during precipitation events. The nearest upper air station, operated by Environment Canada, is Prince George, located about 100 kilometres south of the study region. The 700 millibar wind record was obtained for the period of 1980 to 1990 and categorized according to eight cardinal directions. Precipitation data were then obtained for the same period for Mackenzie, an Environment Canada station within the basin for which the climate record is continuous for the same period as the upper air station. None of the B.C. Hydro

stations has an unbroken daily record for that period.

According to this analysis, roughly 35 percent of the annual precipitation at Mackenzie falls when the upper winds at Prince George are less than 10 knots which is typical of spring and summer. Roughly 55 percent of the annual precipitation occurs when the winds are stronger, above 10 knots, and when the upper wind direction is from the west (24 percent), southwest (21 percent), or south (11 percent). Such winds tend to be more typical of fall and winter. The remaining 10 percent of precipitation is accounted for by winds ranging from northwest clockwise through southeast.

Results

Simple linear regression of elevation and slope on precipitation was performed for a typical winter month, January, and a typical summer month, July. Five individual years between 1986 and 1990, as well as the average of these five years, were used in the study. By choosing individual years, the largest sample is obtained since the number of stations is maximized. Conversely, by choosing a five year average, the variability is reduced, but the sample is much smaller because only a few stations have a five-year period of record in common. The analysis was then extended from monthly to seasonal data by aggregating precipitation totals for June, July and August, into five year averages. Regression analysis was performed on the entire set of available data, then on subsets of data according to aspect. In analyzing the relationship between precipitation and slope, only slopes greater than or equal to 5 metres per kilometre are included to eliminate flatter terrain.

The two accompanying tables are divided into three sections: station elevations, DEM elevations and slope. Under each section, the results are first shown for all data followed by the results of partitioning the data according to aspect. A number of selected scatterplots are included for illustrative purposes. Data points are labeled for map reference.

January: individual years from 1986 through 1990: Table 2 shows correlation coefficients for five individual Januarys from 1986 through 1990 as well as the five-year average. The number of stations varies from 18 to 24.

With the exception of the year 1989, there does not appear to be a strong and consistent relationship between January precipitation and either station elevation or DEM elevation for the unpartitioned data. When aspect was taken into account, correlations remained generally low, and the precipitation-elevation relationship was evident in only a few cases. In 1989 the correlation between precipitation and DEM elevation is greater than 0.7 for north, east, and west aspects, but not south. Despite the high values, only east aspect is statistically significant at the 95 percent confidence level for 1989 because of the small sample size. In some cases, the elevation-precipitation relationship is inverse as indicated by the negative correlations for north aspect in 1988 with both station elevation and DEM elevation. Overall, DEM elevation does not appear to be more strongly correlated with precipitation than does station elevation with respect to individual Januarys.

The relationship between slope and precipitation is quite inconsistent across all years with almost as many negative correlations as positive irrespective of aspect. Only two statistically significant correlations between slope and precipitation were obtained: a positive correlation for north aspect in 1989 and an inverse relationship for west aspect in 1990.

January five year average, 1986 to 1990: Six stations were found with good January data for 1986 to 1990. Of these six, four had east aspects. An analysis of these four indicates strong, but not significant ($p<.05$) correlations between station elevation and DEM elevation and precipitation, as well as between slope and precipitation. The relationship between DEM elevation and precipitation is stronger than that of station elevation based on this rather small sample. Scatterplots of these data using five year averages are shown as Figures 3 and 4.

July: individual years from 1986 through 1990: As shown in Table 3, a much stronger relationship between elevation and precipitation was found using July data than with the January case. The sample size is slightly larger ranging from 21 to 26 stations. Both DEM elevation and station elevation appear to be about equally correlated with precipitation. Of the five individual years, only 1987 stands out as a poor example. The other four years show either station elevation or DEM elevation to be significantly correlated with

TABLE 2. JANUARY (1986-90). Correlation coefficients of monthly precipitation vs. station elevation, DEM elevation, and slope, individual years and a five year average, with stations taken as a whole and partitioned according to aspect. Statistically significant ($p<.05$) correlations are indicated by bold italics.

	1986	1987	1988	1989	1990	Five Year Aver.
Station elevation						
All aspects	-.13	.03	-.27	.40	.18	.69
	N=19	N=19	N=18	N=24	N=19	N=6
	p=.58	p=.90	p=.28	p=.06	p=.46	p=.13
North aspect	n/a	-.28	-.90	.69	.35	n/a
	N=2	N=5	N=3	N=6	N=5	N=0
		p=.65	p=.29	p=.13	p=.56	
East aspect	-.26	.09	-.37	.15	.64	.51
	N=7	N=6	N=7	N=7	N=76	N=4
	p=.58	p=.87	p=.41	p=.75	p=.17	p=.49
South aspect	.22	.76	.83	.27	.89	n/a
	N=6	N=5	N=4	N=7	N=4	N=1
	p=.68	p=.14	p=.17	p=.55	p=.11	
West aspect	.50	.89	.01	***.99***	-.32	n/a
	N=4	N=3	N=4	N=4	N=4	N=1
	p=.50	p=.30	p=.99	p=.00	p=.68	
DEM elevations						
All aspects	.08	.13	-.18	***.48***	.03	.69
	N=19	N=19	N=18	N=24	N=19	N=6
	p=.74	p=.61	p=.46	p=.02	p=.92	p=.13
North aspect	n/a	-.26	-.95	.74	.27	n/a
	N=2	N=5	N=3	N=6	N=5	N=0
		p=.68	p=.20	p=.09	p=.66	
East aspect	.35	.19	.23	***.79***	.47	.87
	N=7	N=6	N=7	N=7	N=6	N=4
	p=.44	p=.72	p=.62	p=.04	p=.35	p=.13
South aspect	.22	***.92***	.82	.24	.11	n/a
	N=6	N=5	N=4	N=7	N=4	N=1
	p=.67	p=.03	p=.18	P=.60	P=.90	
West aspect	-.06	.79	-.30	.80	-.57	n/a
	N=4	N=3	N=4	N=4	N=4	N=1
	p=.94	p=.42	p=.71	p=.20	p=.43	
Slope						
All aspects	.17	-.04	.50	.35	-.21	
	N=16	N=14	N=14	N=18	N=15	
	p=.54	p=.90	p=.07	p=.15	p=.46	
North aspect	n/a	.91	n/a	***.96***	.32	n/a
	N=2	N=3	N=1	N=4	N=3	N=0
		p=.28		p=.04	p=.80	
East aspect	.66	-.16	.70	.47	.28	.81
	N=7	N=6	N=7	N=7	N=6	N=4
	p=.11	p=.76	p=.08	p=.29	p=.59	p=.19
South aspect	-.02	n/a	n/a	-.29	n/a	n/a
	N=3	N=2	N=2	N=3	N=2	N=1
	p=.99			p=.82		
West aspect	-.54	-.41	.02	.22	***-.95***	n/a
	N=4	N=3	N=4	N=4	N=4	N=1
	p=.46	p=.73	p=.98	p=.78	p=.05	

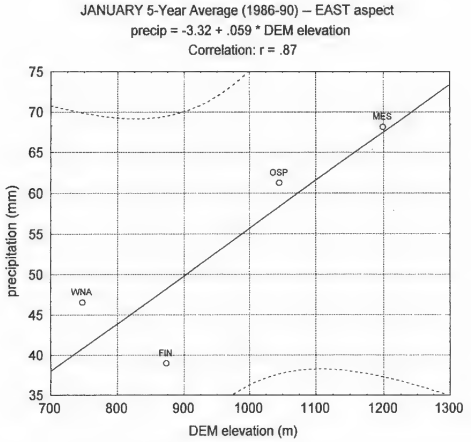

Figure 3. DEM elevation vs. JANUARY five-year average (1986 to 1990) precipitation for stations with EAST aspect.

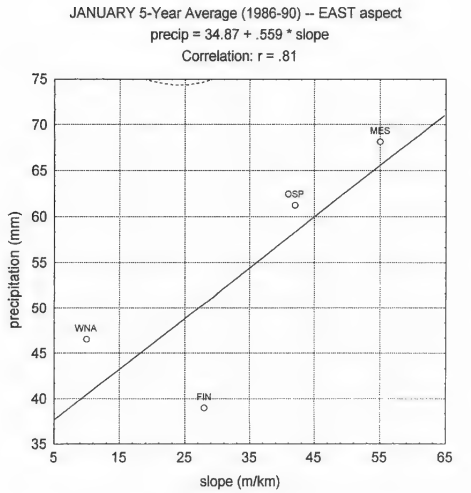

Figure 4. Slope vs. JANUARY five-year average (1986 to 1990) precipitation for stations with EAST aspect.

precipitation without further segmentation of data according to aspect.

When the data are partitioned according to aspect, the most noticeable effect is that, in general, precipitation at stations with either north or east aspects tends to be highly correlated with both categories of elevation. The elevation-precipitation relationship involving south and west aspects tends to be uniformly poor and in some cases negative. Regarding slope, there does not appear to be any relationship with precipitation, and there are nearly as many negative as positive correlations regardless of aspect.

July, 1989 was examined in detail. Scatterplots are included as Figures 5(a) to 5(d) and show the relationship between DEM elevation and precipitation by aspect. Of the 26 stations, five have north aspects, eight are east, eight are south and five are west. The best correlations are with north and east aspects.

To attempt to explain a physical basis for these results, 700 millibar wind data were examined for July, 1989. Morning and afternoon soundings show the winds to be light, less than 10 knots, and variable most days of that month. This is a typical summer wind pattern for Williston Basin, and precipitation is usually the result of convective activity at this time of year. Accordingly, the concept of orographic enhancement occurring as a result of large scale ascent by topographic forcing may not be valid in this case. In the absence of wind, a more likely mechanism for the occurrence of precipitation may be the formation of convective clouds on sunny mountain slopes. However, it is not known why a stronger precipitation-elevation relationship would be found on north and east facing slopes.

July five year average, 1986 to 1990: Sixteen stations with July data for the period were found. Stations with either east or south aspects demonstrated moderately strong correlations between station elevation and precipitation although only one was significant at the 95 percent confidence level. DEM elevations appear to be somewhat better correlated with precipitation than are station elevations. Stations with west aspect showed high negative correlations, however, the sample includes only three stations. Slope and precipitation are all negatively correlated according to this rather small sample. Scatterplots of the five year average for July are included as Figures 6(a), 6(b) and 7.

Summer, five year average, 1986 to 1990: The results of a five year average of total precipitation for the combined months of June, July and August are shown in Figure 8. Only 10 stations have data for this five year period. Of these ten, one has a north aspect, six are east, two are south, and one is west. Only stations with east aspect are shown in the figure. The scatterplot obtained

TABLE 3. JULY (1986-90). Correlation coefficients of monthly precipitation vs. station elevation, DEM elevation, and slope, individual years and a five year average, with stations taken as a whole and partitioned according to aspect. Statistically significant (p<.05) correlations are indicated by bold italics.

	1986	1987	1988	1989	1990	Five Year Aver.
Station elevation						
All aspects	***.64***	.02	.29	***.38***	***.57***	***.68***
	N=21	N=23	N=21	N=26	N=23	N=16
	p=.00	p=.91	p=.20	p=.05	p=.01	p=.00
North aspect	.86	***.94***	-.60	.68	.70	n/a
	N=4	N=4	N=4	N=5	N=5	N=2
	p=.14	p=.05	p=.40	p=.20	p=.19	
East aspect	***.91***	-.01	.42	***.95***	***.92***	***.87***
	N=6	N=7	N=8	N=8	N=8	N=6
	p=.01	p=.99	p=.30	p=.00	p=.00	p=.02
South aspect	.35	-.16	.09	.16	-.03	.55
	N=7	N=7	N=5	N=8	N=6	N=5
	p=.45	p=.73	p=.89	p=.70	p=.95	p=.34
West aspect	-.26	-.04	-.34	-.22	-.27	-.98
	N=4	N=5	N=4	N=5	N=4	N=3
	p=.74	p=.94	p=.66	p=.72	p=.73	p=.14
DEM elevations						
All aspects	.29	-.09	***.50***	***.53***	***.43***.	.37
	N=21	N=23	N=21	N=26	N=23	N=16
	p=.20	p=.67	p=.02	p=.01	p=.04	p=.15
North aspect	***.97***	.93	-.67	.74	***.88***	n/a
	N=4	N=4	N=4	N=5	N=5	N=2
	p=.03	p=.07	p=.33	p=.15	p=.05	
East aspect	.60	-.17	.64	***.73***	***.75***	.62
	N=6	N=7	N=8	N=8	N=8	N=6
	p=.21	p=.72	p=.09	p=.04	p=.03	p=.19
South aspect	.26	-.02	-.28	.40	-.30	.63
	N=7	N=7	N=5	N=8	N=6	N=5
	p=.57	p=.96	p=.65	p=.33	p=.56	p=.25
West aspect	-..81	-.35	.27	.28	.28	-.90
	N=4	N=5	N=4	N=5	N=4	N=3
	p=.19	p=.56	p=.73	p=.64	p=.72	p=.28
Slope						
All aspects	-.23	.02	.33	.10	-.05	-.07
	N=16	N=17	N=17	N=20	N=18	N=12
	p=.39	p=.95	p=.20	p=.66	p=.86	p=.83
North aspect	.74	n/a	-.06	.53	.40	n/a
	N=3	N=2	N=3	N=3	N=3	N=1
	p=.47		p=.96	p=.61	p=.74	
East aspect	-.57	.07	.17	-.36	-.32	-.27
	N=6	N=7	N=8	N=8	N=8	N=6
	p=.24	p=.88	p=.68	p=.38	p=.43	p=.60
South aspect	.01	.72	n/a	.60	-.14	n/a
	N=3	N=3	N=2	N=4	N=3	N=2
	p=.99	p=.49		p=.40	p=.91	
West aspect	-.32	-.74	.50	.25	.67	-.41
	N=4	N=5	N=4	N=5	N=4	N=3
	p=.68	p=.16	p=.50	p=.69	p=.33	p=.73

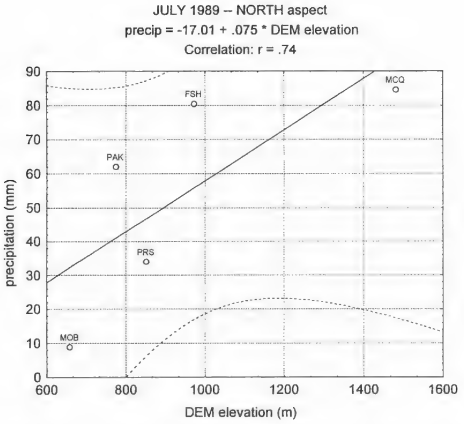

Figure 5(a). DEM elevation vs JULY 1989 precipitation for stations with North aspect.

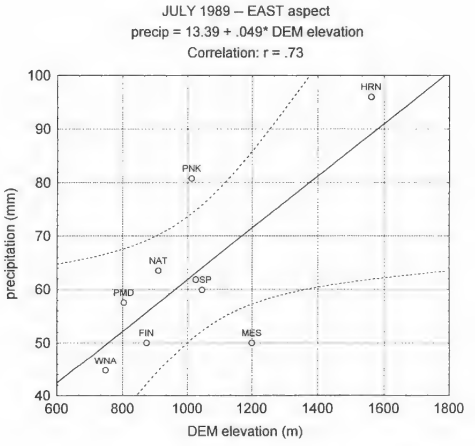

Figure 5(b). DEM elevation vs. JULY 1989 precipitation for stations with EAST aspect.

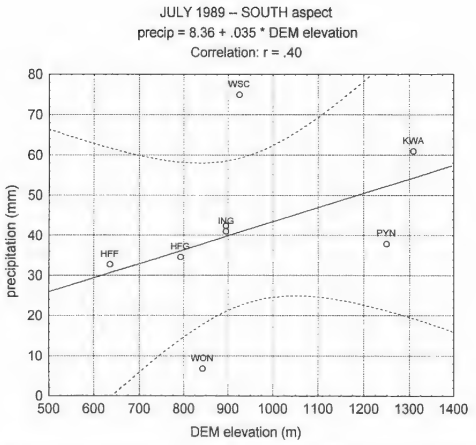

Figure 5(c). DEM elevation vs. JULY 1989 precipitation for stations with SOUTH aspect.

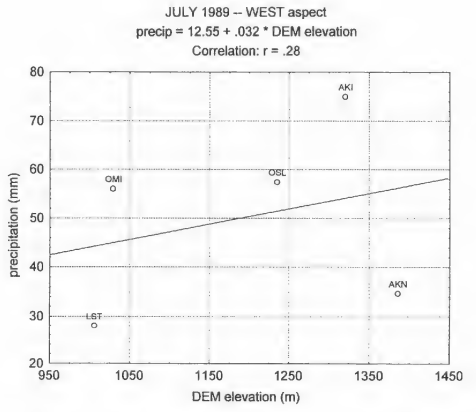

Figure 5(d). DEM elevation vs. JULY 1989 precipitation for stations with WEST aspect.

using June/July/August data is very similar to that obtained when only July data are used for the same five year period.

Conclusion

The aim of this study was to determine statistical relationships between precipitation and orographic parameters such as elevations slope and aspect in the Williston Basin. At the present time, however, the development of a suitable statistical model is limited by the lack of good quality data. The most encouraging result of this study was a crude relationship between summer precipitation and elevation for terrain having north or east aspects. Individual months appear to provide a better basis for statistical modelling than five-year monthly averages, mainly due to the reduced sample size arising from missing data as the period of record is increased. Because of high interannual variability, a statistical model based on individual years of data would be limited in its applicability to other years. In order to have more universal application, perhaps 10 to 20 more years of data would need to be collected in order to mitigate the trade-off between sample size and length of record. This is especially true when partitioning

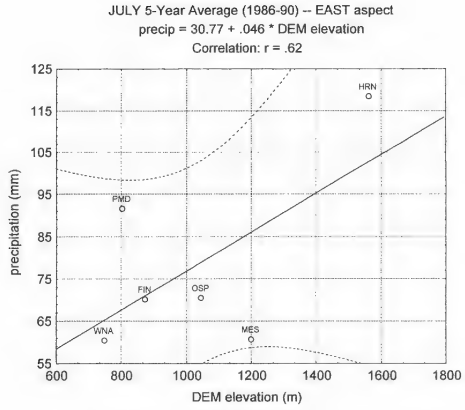

Figure 6(a). DEM elevation vs. JULY 5-year average (1986-90) precipitation for stations with EAST aspect.

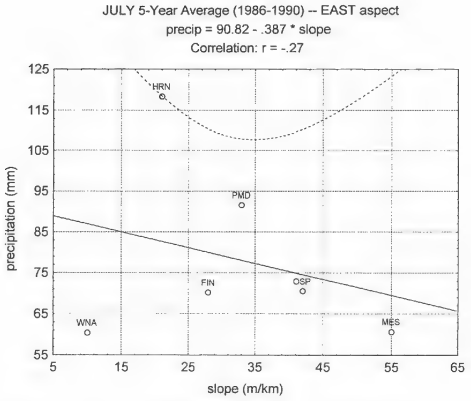

Figure 7. Slope vs. JULY 5-year average (1986-90) precipitation for stations with EAST aspect.

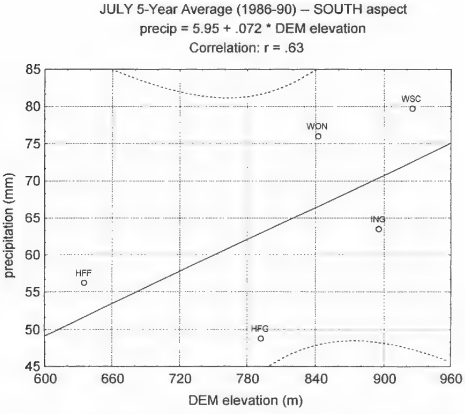

Figure 6(b). DEM elevation vs. JULY 5-year average (1986-90) precipitation for stations with SOUTH aspect.

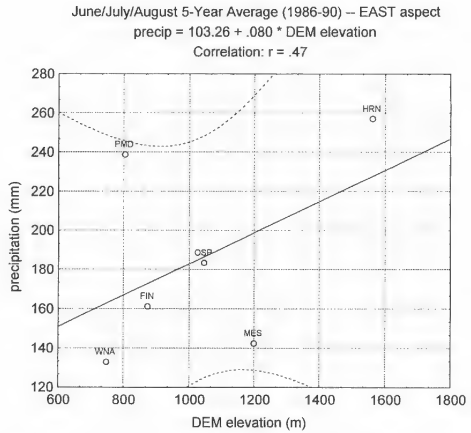

Figure 8. DEM elevation vs. total June/July/August five-year average precipitation (1986 to 1990) for stations with EAST aspect.

the data according to aspect into still smaller subsets.

Given the extent of underreporting of snow in Williston Basin, as in other mountainous regions, the opportunities to statistically model orographic effects during the winter period are severely limited. This problem is being addressed by B.C. Hydro through the conversion of its network to the larger standpipe type of gauge. However, several years of data using new instrumentation would be needed to reach any conclusions about the orographic enhancement of snow in this basin. For GEWEX purposes, statistical modelling would necessarily be limited to summer precipitation due to the questionable quality of the winter precipitation data.

According to this study, the precipitation-elevation relationship appears to be just as valid for station elevations as for DEM elevations. This is in contrast to other studies which showed coarser scale elevations to be better correlated with precipitation than point elevations. No consistent relationship between precipitation and slope was found.

Within these limitations, it would appear that any of the interpolation techniques discussed

earlier, including kriging and PRISM, may be appropriately used with summer precipitation data. The study did not attempt to geographically stratify the data according to different climate regimes, and if the Williston basin is not characterized by a single orographic regime, then some means of dividing the region into sub-regions would have to be done prior to performing kriging. One of the strengths of the PRISM model lies in its ability to continuously adjust its frame of reference to local precipitation-elevation relationships, thereby enabling it to maintain its accuracy over large non-homogeneous regions. Regardless of the technique chosen, the quality of the precipitation data will continue to be a limiting factor in the accuracy of the model results.

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Northwest Science Forum

Northwest Science Forum provides an opportunity to articulate and discuss scientific issues in a less structured format than peer-reviewed articles. The Forum publishes short articles, opinion pieces, and letters with a focus on science and natural resource issues in the Pacific Northwest. Although the Forum is not peer-reviewed, it is edited for format and clarity. Articles should generally be less than 2000 words and contain minimal literature citations. Letters in response to articles are particularly encouraged; the original author will normally be given a chance to respond to the letter as well. There are no page charges or reprints associated with the Forum, and participants need not be members of the Northwest Scientific Association. Please send all submissions, including two hard copies and an electronic copy (any recent version of Word or WordPerfect, Macintosh or DOS), to the Editor.

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A Comment on the Future Environmental Status of Coeur d'Alene Lake, Idaho

Abstract

Coeur d'Alene (CDA) Lake sits some 80 km downstream of the Bunker Hill lead-zinc smelter complex in northern Idaho, a scenic region that is experiencing rapid population growth. As a result, there is some concern about future eutrophication and the relationship between that and the fate of dissolved and particulate heavy metals introduced to the lake via largely historic mining and smelting activities upstream. Based on recent research, the United States Geological Survey (USGS) has concluded that "most" of the metals in the sediments of CDA Lake are associated with iron oxides. Because such phases are soluble under anoxic conditions, concern has been expressed that depletion of oxygen from the deep waters in the future could permit the release to the lake waters of a significant fraction of the metals currently sequestered by the sediments, and this could have unwelcome environmental consequences. This suggestion has been published in the open scientific literature and it appears to have been accepted uncritically by an array of government entities and concerned parties. I argue here that the conclusion that "most" of the metals are associated with oxides is not supported by the data collected by USGS personnel, which invalidates the extrapolated concern about metal release. A more serious environmental insult would appear to be oxygen depletion *per se*, which is likely to occur if increased residential development is allowed to reverse the decline in nutrient inputs that has occurred over the past 15 years.

Introduction

Mining and smelting activities have been conducted for more than a century in the watershed of the Coeur d'Alene River in northern Idaho. As a result, the waters of Coeur d'Alene (CDA) Lake have for many years hosted lead and zinc concentrations well above natural levels. Recent work by the United States Geological Survey (USGS) has shown that, in addition to the water column, the sediments in the south-central part of the lake are relatively enriched in a number of metals including copper, cadmium, lead, and zinc (Horowitz et al., 1993). Chemical extractions of the deposits have been made in an effort to determine the mode of occurrence of the metals, i.e. are they adsorbed onto particle surfaces or have they been precipitated in various discrete mineral phases that form as a result of post-depositional chemical reactions? (A third option is that the enrichments simply represent the deposition of metal-rich particles that have been carried to the lake by local rivers). Determination of the mode of occurrence is fundamental to any attempt to predict the potential future behaviour of the metals. For example, by determining whether or not the metals are coupled to certain oxide minerals or phases in the sediments, it might be possible to forecast the extent of release or uptake under certain water quality scenarios for Coeur d'Alene Lake.

One of the principal conclusions offered by Horowitz et al. (1993) is that "most of the enriched trace elements...are associated with an operationally defined Fe (iron) oxide phase". If true, such an association represents a pool of metals that could be released to the overlying lake water should future eutrophication cause the oxygen concentration to be fully depleted in deep waters. Taken at face value, this could have a temporary negative impact on water quality. However, the term "operationally defined" is critically important in drawing such a conclusion, because it refers to the experimental conditions used in the laboratory to distinguish the apparent metal-iron oxide association, and not actual conditions in the field. The results of such experiments are notoriously difficult to interpret, and they typically yield conclusions that are equivocal. The controversial nature of such work is not well known to scientists outside this field of research, and this can lead to misinterpretations of the original results. For example, the cautious but scientifically ambiguous term "operationally-defined iron oxide-metal associations" used by Horowitz et al. (1993) was incorrectly interpreted by the authors of the CDA Lake Management Plan (November, 1994, p. 23) who state conclusively that, "The vast majority of the [sedimentary] trace elements were associated with iron oxides...". It will be shown in this comment that the sample handling and laboratory techniques used by USGS personnel cast serious doubt on the validity of this conclusion. Without more scientifically rigorous and thorough research, the association imputed between oxides and metals must be viewed as speculation.

Critical Review of Previous Work

Background

An ordered sequence of post-depositional chemical reactions occurs naturally in lake sediments, and is driven by the decomposition of organic matter by bacteria. Assuming that the bottom water in the lake contains dissolved oxygen (the usual condition in most lakes year-round), organic matter on the lake floor will first be decomposed ("oxidized") by aerobic bacteria to produce carbon dioxide and water, amongst other metabolic products. Oxygen (O_2) is consumed during this reaction. Some of the organic matter that settles to the lake floor gets buried in the sediments, and supports continued bacterial metabolism below the sediment-water boundary. If the consumption of oxygen by aerobes in shallow subsurface sediments exceeds the rate at which O_2 can migrate downward to replace that used, the oxygen content falls to zero at some sub-bottom depth. This usually occurs in lake sediments within the upper several centimetres. Once oxygen is depleted, different bacterial communities continue decomposing organic matter by taking advantage, in sequence, of the oxygen present in different "oxidizing agents". In preferred order, these are nitrate (NO_3^-), manganese oxides, iron oxides, and sulfate (SO_4^{2-}). Important products of the decomposition reactions in the sediments are dissolved manganese, dissolved iron, and dissolved hydrogen sulphide. Thus, with increasing depth in the pore waters in the sediments, an observer could expect to see, in order, the disappearance of oxygen, the disappearance of nitrate, the appearance of dissolved manganese, the appearance of dissolved iron, and the appearance of dissolved hydrogen sulfide.

There are some complications in this basic picture, however. Dissolved manganese and iron both react with oxygen to form their respective oxides. The upward migration of the dissolved elements through the pore waters from the depths at which they are released to solution will support precipitation of manganese and iron oxide phases near the sediment-bottom water interface where dissolved O_2 is present. Over time, as sedimentation continues, these oxides get buried, only to be redissolved and again migrate upwards to repeat the cycle. This "diagenetic cycling" phenomenon causes the oxides to accumulate just below the sediment-water interface, in the so-called "aerobic zone". In much of Coeur d'Alene Lake this zone appears to be <1 to ~3 cm thick, based on available data.

Manganese and iron oxides effectively adsorb a wide range of dissolved metals from solution. The trace metals, zinc and lead, for example, can be adsorbed onto such phases near the sediment surface, and released to solution upon burial and dissolution of the oxides. This will support upward migration of the dissolved trace metals, and possible release to the overlying lake water, although this will be countered by readsorption onto freshly-precipitating manganese and iron oxides in the aerobic zone. Thus, metals such as zinc and lead tend to cycle, at least partly, with the major oxide phases during diagenesis

In the natural aging cycle of lakes, progressive infilling leads gradually to increases in dissolved nutrients which support the growth of plankton. Human activities, such as the input of sewage or runoff from agricultural areas, can greatly accelerate this natural process. Such "artificial" inputs can increase the plankton growth to the point where the enhanced settling of dead organic matter to the lake floor leads to oxygen depletion in the deep waters. One consequence of this is clear: the oxide phases in the surface sediments will dissolve progressively when the aerobic zone disappears, potentially releasing dissolved metals directly to the lake water. It is for this reason that the USGS thought it important to determine the proportions of zinc and lead that are associated with oxides in Coeur d'Alene Lake sediments. In the following section, the approach used by USGS scientists to make such determinations is critically assessed.

Chemical Extraction Studies

It is very difficult to determine with any degree of confidence the proportions of trace metals associated with various components in aquatic sediments. Most investigators who attempt such studies use the sequential extraction scheme developed about seventeen years ago by Andre Tessier and his colleagues (Tessier et al., 1979). In the application of the method, a sediment sample is subjected to a progressive five-step chemical attack in which the sample is exposed to increasingly stronger chemical compounds. The amounts of the trace metals of interest removed at each step are determined by chemical analysis of the extract solutions. Five fractions among which a given trace metal may be partitioned are defined by the approach of Tessier et al (1979):

1. Exchangeable fraction: includes metal ions loosely sorbed on particle surfaces, extracted using $MgCl_2$ or sodium acetate solutions at room temperature and at neutral pH.

2. Carbonate fraction: includes metals associated with carbonate phases, and thus susceptible to release under acid conditions. This fraction is extracted by exposing the residue from step 1 to a weak acetic acid-sodium acetate solution at room temperature.

3. Iron- and manganese-oxide-bound fraction: includes metals strongly adsorbed by oxides. The residue from step 2 is attacked with hydroxylamine hydrochloride in acetic acid at 96 °C. This is a chemically reducing solution which is designed to mimic the anoxic (oxygen-free) conditions seen in natural sediments below the aerobic zone.

4. Organic-matter-bound fraction: includes trace metals bound to organic matter. The residue from step 3 is exposed to a multi-reagent solution containing HNO_3 and H_2O_2.

5. Residual fraction: the residue from step 4 is fully dissolved in a very strong acid mixture.

One of the major concerns associated with application of the sequential extraction technique is the degree to which the method simulates natural processes. For example, the strong reagents and fast reactions inherent to the approach differ drastically from the weak reagents and slow kinetics typically found in nature. The specificity of the individual reactions is also controversial. The amount of metal extracted at each step is a complex function of the extraction reagent type and concentration, the sequence of application, temperature, exposure time, extent of readsorption, and the solid to solution ratio. Thus, the extracts are termed "operationally defined" (Tessier, et al., 1989), which means that the fractions to some degree reflect the experimental conditions employed, rather than true geochemical partitioning. Nevertheless, partial extractions can be used pragmatically in sediment geochemistry studies if they are applied with discrimination and care. The scientific danger lies in the uncritical use of such techniques and in over-interpretation of the results.

It is very important in partial extraction work to ensure that the integrity of the samples is not compromised by improper collection and handling. For example, exposure of anoxic sediments to the atmosphere can induce perturbations in the natural partitioning of metals. To avoid introducing such artifacts, anoxic sediments should be kept in an anaerobic atmosphere throughout the entire manipulation and extraction procedure.

The approach used by Horowitz et al. (1993) to determine trace metal partitioning in CDA Lake sediments suffers in three areas. First, Tessier et al. devised their scheme for use on oxic, surface sediments, *not* for application to anoxic sub-surface deposits. Second, no effort was made to keep the samples isolated from contact with the atmosphere. Third, application of the partial extraction technique did not follow carefully established

protocols. Near-surface sediments (upper 2 cm) were collected with an Ekman Dredge sampler, and subsampled in air. This may not have chemically biased the samples if the deposits were fully oxidized, but Horowitz et al. (1993, p. 409) note that "many of the samples obtained from the main body of Lake CDA had very thin (of the order of a few millimetres) surface veneers of reddish, fine-grained material...". Iron oxides invariably contribute such a reddish coloration. The absence of this hue just below the surface implies that anoxic conditions are established at very shallow depths. The sediment samples were subsequently kept cool on ice, shipped to Atlanta, and kept cool until processed and analysed sometime later. The processing included stirring (in air) with a glass rod (to homogenize the sample), sieving to remove large material such as wood chips, and freeze-drying. Considering that there is roughly 10,000 times more oxygen in the atmosphere than in lake bottom waters (largely because oxygen is poorly soluble in water), anoxic sediments can be rapidly oxidized when exposed to air, particularly when they are wet. Thus the handling of the samples could have altered their composition, for example by permitting oxidation of metal sulphide minerals. Such effects would bias subsequent extractions and lead to an overestimation of the content of oxide-hosted metals. Even if anoxic sediments remained unoxidized after the many handling steps, the extractions would still produce misleading results. This is because a number of sulfide minerals that are stable under anoxic conditions will be dissolved progressively in steps 2 and 3 of the Tessier et al. method. In order to reduce such uncertainties, a much more rigorous sample handling procedure would be required.

The manner in which chemical extraction techniques were used and interpreted by Horowitz et al. (1993) is problematic. Rather than conduct the five-step procedure designed by Tessier et al. (1979), only two steps were used. In the first, dried unground sample aliquots were exposed to hydroxylamine-hydrochloride in hydrochloric acid (HCl) at 50 °C for thirty minutes. This is similar to the solution used in Step 3 above, and it would have extracted, operationally, exchangeable metals, carbonate-hosted metals, some fraction of the metal inventory hosted by Mn and Fe oxides, and metal monosulfides, which readily dissolve in HCl. Tessier et al. (1989, p. 1516) note that hydroxylamine hydrochloride is reasonably selective in dissolving Fe and Mn from their oxyhydroxide forms, and releasing associated trace metals, *provided that carbonates have been previously removed* (italics added). Since the latter condition was not satisfied, and it is not known whether or not sulfides were present, it is misleading to make the statement, "Most of the lead (~95%) cadmium (~90%), Zn (~80%) arsenic (~75%) and copper (~55%) appear to be associated with an operationally-defined iron oxide phase..." (Horowitz et al., 1993, p. 418). Distinguishing between carbonate, sulphide and oxide hosts is important, because carbonate and sulphide phases will not dissolve under anoxic conditions, but oxides will.

A Point for Reflection

Determining the hosts for metals in contaminated sediments is a difficult scientific problem. In the case of Coeur d'Alene Lake, I suggest that it remains an open question. Even if iron oxides do turn out to be a significant host for metals on the floor of the lake, the postulated release of dissolved metals from the sediments to the overlying water under anoxic conditions remains hypothetical. In my view, the main threat to the future health of the waters and biota of the lake is the development of seasonal anoxia associated with eutrophication. To ensure that this scenario does not develop as a consequence of ongoing development pressures, continuing and perhaps more stringent constraints on inputs of phosphorus will be needed. Control of nutrient fluxes should be the primary focus of current management action in order to ensure that oxygen levels necessary for a healthy lake are maintained.

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The author is grateful to Dr. Dominic di Toro and an anonymous reviewer for their critical reviews of the draft version of this paper, from which this article was condensed.

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Book Reviews

Biodiversity in British Columbia: Our Changing Environment

Harding, L.E. and E. McCullum (editors), 1994, Environment Canada, Canadian Wildlife Service, Ottawa, Ontario, Canada. 426 pp. ($24.95)

Our Living Legacy: Proceedings of a Symposium on Biological Diversity.

Fenger, M.A., E.H. Miller, J.F. Johnson and E.J.R. Williams (editors), 1993, Royal British Columbia Museum, Victoria, B.C., Canada. 392 pp. ($14.95)

British Columbia is one of the most biologically rich areas in the temperate world. A variety of climates (including Canada's wettest and driest) produce a variety of ecological zones and habitats, with six of Canada's ten forest regions represented in B.C. Though the province is 60% forested, it also has extensive grasslands and wetlands, and 18% of B.C. is above treeline. Within our provincial boundaries can be found, for example, 60% of Canada's vascular plant species, 75% of Canada's bryoflora, more than 70% of Canada's bird species, and 80% of Canada's terrestrial mammal species.

Two recent additions to B.C.'s biodiversity literature document this wealth: *Our Living Legacy: Proceedings of a Symposium on Biological Diversity* (OLL); and *Biodiversity in British Columbia: Our Changing Environment* (BBC).

OLL contains papers presented at a symposium on biodiversity held at the Royal B.C. Museum (Victoria, B.C.) in spring 1991. The sessions include Global Values of Biodiversity, Principles of Biodiversity, Diversity in Ecosystems of British Columbia, Diversity at Risk, Strategies (for protecting biodiversity), What Can We Do?, and Public Expectations (a panel discussion). There is also a Keynote Address by David Suzuki ("Biodiversity for the Next Millennium"), Welcoming Remarks, and Foreword. (A good general rule, especially in an field of active research such as biodiversity, is that Proceedings should be published within a year of a conference; in this case, the time from conference to bookshelf was twice that).

BBC contains articles on B.C.'s biodiversity under the headings Introducing Biodiversity, Species Diversity, Ecosystem Diversity, and Prospects for the Future. Approximately 20% of BBC is a compilation of existing information rather than an entirely new product: Chapters 4, 7, 10, 11, and 13-16 are derived, in whole or in part, from Bioline, the newsletter of B.C.'s Association of Professional Biologists; Chapter 1 is from the book *Endangered Spaces: The Future for Canada's Wilderness* (Hummel 1989); Chapter 25 is based on a paper presented at a native plant colloquium; and Chapter 27 is from "Guide to Ecological Reserves in British Columbia". (Reprinting material from fairly obscure sources such as Bioline is an effective way to make it more widely available).

The books have different goals. For OLL, it is "...to address the conservation of biological diversity, ...to summarize current understanding of provincial biodiversity, to communicate provincial responsibility and action... and to place provincial issues in their broad ecological and geographic contexts". For BBC, the goal is "not thoroughly to analyze biodiversity, but rather to identify large scale changes in and emerging threats to it". Because of their different intents, and different formats (symposium proceedings vs. collection of essays), the end result is two very different B.C. biodiversity primers.

BBC has 46 pages (about 11% of the book) of introductory material, covering topics such as development of a conservation ethic, provincial and national systems for listing threatened and endangered species, and taxonomy and nomenclature. OLL has 176 pages (45% of the book) of introductory material, covering topics such as (again) development of a conservation ethic, global biodiversity (and B.C.'s role in the global picture), and principles of biodiversity. The papers by David Suzuki (OLL) and Stan Rowe (BBC) provide thoughtful introductions to both volumes. On the other hand, I do not find the 6 pages devoted to "Welcoming Remarks" in OLL to be terribly useful.

BBC takes a more systematic approach to describing provincial biodiversity, with individual

chapters for most major taxonomic groups (except marine fish, freshwater algae and microbes), followed by chapters for most major ecosystem types (including, oddly, birds and plants!). OLL spends 88 pages (approximately 22% of the book) describing B.C.'s biological diversity and its risk factors; BBC spends 308 pages (72% of the book) on the same topics.

So, we have a very diverse province, and some elements of this diversity (species, ecosystems) are at risk. What do we do about it? OLL devotes 127 pages (32% of the book) to describing risk factors, and proposing strategies. (A 26-page chapter documenting the Panel Discussion is not particularly enlightening.) BBC provides 71 pages (17% of the book) of "Prospects for the Future" (largely confined to protected areas, alas; OLL has more in the way of strategies for the landbase outside of protected areas, which is where biodiversity will be saved, or lost).

There is a mega-diversity of books about biodiversity on the market these days. The primary reason people write books about what we know about biodiversity, I think, is that books about what we do *not* know about biodiversity would be too long. Both OLL and BBC discreetly steer clear of topics such as microbial diversity, terrestrial and freshwater algal diversity, and genetic diversity (though OLL has a 14-page Chapter entitled "Secret Extinctions: the Loss of Genetic Diversity in Forest Ecosystems").

So, if you are interested in finding out how many species of reptiles (at least 16) live in B.C., then BBC is your book. If you are more concerned with how we are caring for the lizards, then OLL might be a better reference. And if you are interested in some basic background reading on B.C.'s biodiversity, these two complementary volumes are a good place to start.

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A Common Fate: Endangered Salmon and the People of the Pacific Northwest
Joseph Cone, Henry Holt and Company, New York, 1995. 340 pages (Cloth, $25.00)

The salmon of the Pacific Northwest are in crisis. Hardly anyone needs to be told that basic fact. But the complexity of the issues surrounding the crisis, its historical roots, a chronicle of the personal values and commitment of many of the participants, and a glimpse at a possible way out are all well worth the telling. Science writer Joe Cone, Director of Communications for the Sea Grant Program at Oregon State University, has done that, and done it effectively. In 1991 Cone produced a series of radio reports under the title "Endangered Salmon: A Radio Chronicle of the Emerging Crisis". In preparation for that series he carried his tape recorder around Oregon, attending many meetings and interviewing a number of key participants. In this book he has greatly expanded the scope of that successful effort and has supplemented it with many more personal interviews and with research on the history of salmon management and water development in the Northwest.

Cone illuminates the conflict through the eyes of the protagonists. His interviews and time spent with many of the influential players in the drama have given him the ability to present an exceedingly complex issue so that it can be understood by the lay reader. The influences of dams, habitat degradation, overharvest, and hatcheries are well described. Individual participants are widely quoted in the book, giving it the persona of those directly involved, rather than that solely of the writer. It is a very personal history of the decline of salmon in the Northwest. The writer has captured the complexity of the issues and provides a wide variety of viewpoints. The focus is on the Columbia River, but problems on the coast are not neglected. Two dozen or more of the principals provide a cross section, and many other players are mentioned briefly. They come from varied backgrounds: biologists with the U.S. Forest Service and other resource management agencies, commercial fishermen, lawyers, politicians, representatives of environmental organizations, managers facing decisions under the Endangered Species Act, industrial customers of the Columbia River's resources, Native Americans. And Cone has gone beyond the current manifestations of conflict to carefully research the history of the salmon fisheries and their management, or lack thereof.

The six chapter titles provide a flavor of the treatment: Denial and Engagement, introducing the scope of the problem; Conflict, detailing some of the most contentious differences of view; Crisis, laying out the plight of the salmon from the time of the earliest fishers to the present; Questions of Values, where the background for conflict becomes more clear; Hope and Dread, exemplifying the range of future possibilities; and finally, A Common Fate, in which the interdependence of the salmon and the people of the Northwest is made clear. To me, one of the strengths of the book is the way in which it effectively depicts this interdependence, from the time of the first inhabitants to the present. This close connection provides at once the source of the problem and the seeds of a solution. The writer presents lessons in biology and habitat requirements of the fish, along with insights into sociology and economic necessities of their human coinhabitants, including a sensitive treatment of the native American perspective. Toward the end of the book and in the Epilogue he suggests a way ahead, a focus on the interdependence of salmon with the watersheds in which they live. Included are a few examples of what seem to be successful efforts in watershed restoration, especially those involving cooperation between private landowners and local public agencies—a locally based strategy for restoring the health of the ecological systems and the species on which they depend.

The author generally succeeds in making his points. The personal approach is an unusual one for such a complex topic, but it lends a sense of urgency and a broad overview that might be difficult to achieve in a conventional treatment. If there were criticism, it might be that the players are not chosen from the whole team (almost all of the perspectives come from Oregonians) and that the playing field is larger than indicated. Interstate and international rivalries, based on historical participation in the common fishery of the West Coast, provide additional complexity to the conflict. There is only very brief mention of the Pacific Salmon Treaty (with Canada) and none at all of the role of Alaskan catch of Northwest

salmon in the current crisis. On the editorial aspects of the book, I found it quite free of error, but with one mildly annoying idiosyncracy. The end notes citing sources are neither keyed to page numbers in the text nor to footnotes, making them tedious to locate. But these are minor complaints. On balance the book is well written and accomplishes its goal.

It is difficult to be optimistic about the prospects for return of salmon to a place of abundance in the Pacific Northwest or perhaps even to believe that they will persist in any numbers at all, particularly in the Columbia River basin. But clearly, if either is to happen, all elements of society will need to be well informed and to participate in the process. This book is an effective contribution to those efforts. It deserves careful reading by anyone concerned about our common fate.

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Urban Forest Landscapes- Integrating Multidisciplinary Perspectives

Gordon A. Bradley (editor), University of Washington Press, Seattle, WA, USA. 225 p. ISBN 0295-97439

There is a paucity of information on the structure, function, and dynamics of ecosystems within urban landscapes, presumably because urban areas traditionally have not been viewed as ecological systems. For example, few data sets have been compiled on basic ecological information such as the distribution, composition, and dynamics of plant and animal populations, and nutrient cycling processes. Confounding this lack of ecological understanding is the multifarious "landscape" of human built environments, social structures, and behavior that when projected on the "ecological landscape" result in a complex system that is difficult to manage and study.

For these reasons I was excited to learn that a book about "urban landscapes" would be published. A text is urgently needed to synthesize what already is known about urban landscapes, identify gaps in knowledge, and suggest approaches to plan for and manage these systems. However, I found myself disappointed, not because this is a bad book, but because from an ecologist's perspective the content did not live up to the book's title. What I expected was a book on urban landscapes, their structure and function from ecological and human perspectives, and a discussion on future directions in the practice and science of urban forestry. Instead, the book discusses the planning and management of urban tree and wildlife resources, and their costs and benefits from the perspective of several urban forestry-related disciplines. The book does a commendable job in this regard. Accordingly, it is weighted heavily toward the social sciences and the management of natural resources in urban environments; there is little discussion of spatially explicit considerations of landscape structure and function as has occurred for less human modified systems in the field of landscape ecology.

The chapters are written by experts from different disciplines, which is reflected in their varied use of terms. This inconsistency reflects an overall problem that has plagued the field of urban forestry since its inception, that is, the need to identify and define terms that are useful to scientists and professionals. Carefully defined terms are essential for communication within disciplines and they are particularly critical for multidisciplinary discourses. For example, what is the ecological definition of an "urban forest landscape," "urban forest," or "urban ecosystem?" What do the terms "landscape," "forest" and "ecosystem" refer to in an urban context? Does the structure of vegetation in an urban landscape represent a "forest" or "savannah?"

The lack of information on landscape attributes despite the book's title is indicative of this problem. Moreover, the varied uses of these and other terms by contributing authors confuses the reader and hampers integration of the book's chapters. For example, some authors define "urban forests" or "urban forest ecosystems" but from the perspective of their respective disciplines; there is no attempt to use these terms in a manner that is consistent with other chapters. In fact, such terms are used interchangeably within several chapters.

The book is organized into four parts, with chapters being presentations from a meeting with the same title as this volume that was held in 1992 at the Center for Urban Horticulture at the University of Washington. The four parts are: 1) Introduction and Historical Perspective, 2) The Environmental Setting, 3) Special Purpose Landscapes, and 4) Integration: Tradeoffs and Benefits. The references for each chapter, which in many cases are scarce, are appended to it. There are no introductions to the different parts, and chapters do not reference or integrate other chapters in the book. In several instances, authors of separate chapters contradict one another. For example, in *Part II, Chapter 8*, the author questions the usefulness of cost-benefit analyses to increase spending on urban forestry programs, while in *Part IV, Chapter 17*, the author promotes cost-benefit analysis as a means of justifying spending on urban forestry programs. In general, the writing and construction of chapters is adequate; however, *Chapter 3* includes figures that are not referred to in the text, nor do they have captions.

The primary purpose of this book was to promote a multidisciplinary approach in reconciling varied uses of the "urban forest." Because most chapters focus on the Pacific Northwest and California, a large body of knowledge from other urban

metropolitan areas around the country is lacking. *Part I* is a loose collection of three chapters that introduce the subject and provide a historical context. The first chapter sets the tone for the remainder of the book by focusing, to the book's advantage, on a broad spectrum of disciplines and components of urban landscapes, and not on individual-tree management, which is a discipline that has dominated the field of urban forestry since its inception.

Part II comprises six chapters that examine the social, political, economic, and ecological settings from which urban forestry programs emerge. Only *Chapter IV* deals with the ecological component of the "urban forest landscape," while the remaining chapters consider social and economic issues and "how to" strategies for controlling urban development. *Part II* would have benefited from one or two chapters devoted to the structure and dynamics of vegetation in urban landscapes, and a chapter that integrates the "social" and "ecological landscape" in urban and suburban areas.

Part III has six chapters describing the various purposes for which "urban forest landscapes" can be managed, including scenic values, woodland and wildlife management, energy and water conservation, and fire prevention. The chapters on scenic values, forest remnants, wildlife habitat design, and energy conservation are particularly informative; still, there is little ecological information from which the authors can draw. For example, the chapter on the management of forest remnants focuses on the smallness of urban forest patches without considering the surrounding landscape in which these patches are located. Should we expect these forest patches to differ from patches embedded within agricultural landscapes? What about potential introductions of nonnative species from surrounding urban land uses? How does pollution that is generated in urban areas affect adjacent forest ecosystems? That these and other questions are not considered is not surprising as there is little information in the literature on the effect of urban land use on adjacent forest patches. It would have been useful for each author to alert the reader to existing gaps of knowledge in his or her respective discipline.

The chapters in *Part IV* integrate preceding material by focusing on the sustainability of "urban forest landscapes," though the term "sustainability" is never defined clearly. A chapter highlighting a case study on managing the multiple benefits of urban forests is particularly insightful because it broadens the concept of urban forestry to include not only street tree management but also greenbelt management, wildlife enhancement, naturalistic landscaping, and ecological resource management. The final chapter summarizes the book and offers suggestions on managing "urban forest landscapes."

This is an informative book that represents a good start in synthesizing our knowledge of urban landscapes, though the title will lead some readers to expect more information from an ecological perspective. It contains sound advice for managers, planners, and policymakers, and ecologists will appreciate the much needed introduction to the human component of ecosystems.

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Serengeti II: Dynamics, Management, and Conservation of an Ecosystem
A.R.E. Sinclair and Petet Arcese (editors), 1995, University of Chicago Press, Chicago and London.

Much has changed in the 20 years since "Serengeti: Dynamics of an Ecosystem", edited by Sinclair and M. Norton-Griffiths. New ecosystem dynamics have been played out and a considerable amount of new research warrants a fresh synthesis. The socio-political environment is different, and public perceptions of conservation have changed—there is a wide realization that it is necessary to "preserve intact assemblages of species and their habitats as functioning ecosystems". Unlike the first Serengeti book, which was mainly concerned with ecological principles, "Serengeti II" attempts to fuse two decades of pure research with ongoing conservation programs and, to "advise managers who plan for, and respond to, the social, political, and environmental perturbations that affect conservation policy". The book first sets the framework, then moves up through the trophic levels from with plants and soils to herbivores, predators, humans, and system-level syntheses. There are 29 chapters, written by different sets of authors. Sinclair and Arcese managed to weave these together into a coherent whole.

McNaughton and Banyikwa begin by showing the relevance of process-pattern interactions for biological conservation. Spatial heterogeneity has long been an obvious attribute of this ecosystem, however, the ways that herbivores sort out the complex array of nutritional patch types, and the spatial patterns that herbivores create through their herbivory and nutrient recycling are central to ecosystem function. Dublin's work illustrates that indirect interactions among humans, fire, vegetation, herbivores, and climate over decades, may render assumptions of ecosystem steady-states or equilibria irrelevant. In the early 1900's the region was open grassland savanna. Rinderpest, trypanosomiasis and the ivory trade reduced human populations and elephant, with resulting reductions in burning and browsing, and an increase in woody cover through the 1920's and 1930's. Increased human populations, fire, high rainfall, compression of elephants, and low ungulate populations in 1950-60 reduced woody cover, and by 1970-80 conditions resembled those in the early 1900's. Sinclair shows that hypotheses that elephant would eliminate woodlands, that elephant and woodlands would equilibrate, or that elephants and trees would oscillate in a stable limit cycle are inconsistent with data. Though fire was once thought to be the key, recent analyses have show that elephants and fire act together to control system dynamics.

An overview of the status of herbivores is provided in the next two chapters. Population trends and spatial distributions of large herbivores in the region are summarized by Cambell and Borner. Their Serengeti Ecological Monitoring Program has tracked the animals faithfully since 1985. There is a concise description of the methods employed, and how they have developed over time. I found the maps of animal distributions quite informative, and a contour map of the non-migratory wildlife densities clearly shows steep density gradients along protected area boundaries, corresponding closely to the distance that can be covered by a poacher on a one-day foray. Runyoro and colleagues summarize findings of the Ngorongoro Ecological Monitoring Program.. NEMP has reliably followed herbivore populations, however, it is clear that the plant monitoring program could be strengthened. Broten and Said cover monitoring of ungulates in the Mara, to the north. They show the extent of wildlife dependance on lands outside the reserve.

The herbivore studies continue with Sinclair's study of the effect of intraspecific competition vs. predation on non-migratory ungulates. He uses the removal of 85% and 50% of the buffalo in the northern and western Serengeti by poachers as an experimental treatment. While some species increased, others showed no response. Mduma reports a rare study of an uncommon small-bodied ungulate species, the Oribi. Though almost completely absent from aerial survey data, diligent ground counts turned up the highest density ever recorded in Africa! The role of nutrient limitations in the wildebeest migrations is examined by Murray, who rules out calcium, as well as sodium and energy limitations in favor of phosphorus deficiencies on the dry season ranges. Fryxell presents a model which suggests that ungulates should move to the shortgrass plains in preference to more abundant biomass in the tallgrass woodlands because increasing forage biomass is

associated with reduced forage quality, increased handling time, and lower digestible energy intake.

The predators are covered well. FitzGibbon and Lazarus take a process-oriented approach to predation, looking at mechanisms such as grouping, vigilance, and monitoring of detected prey. These behaviors vary among sex, age and condition classes, with important implications for population responses. Scheel and Packer show lions are opportunistic predators, as they must be in an environment where prey densities vary with prey migrations and rainfall. Hanby and Bygot show that in contrast, lions in the Ngorongoro Conservation Area (NCA) experience much more reliable prey densities, and their density is conseqeuently over three times that on the plains. Importantly, they show that the Serengeti woodlands, the plains, and the crater are spatially connected into a single system by virtue of lion emigration and immigration. Hofer and East document the hyena "commuting system", where resident animals exploit migratory prey through long distance hunting exploits. An important consequence of commuting is that hyenas are buffered from temporal fluctuations in migratory prey abundance, unlike most of the other large predators. This means that there are more potentials for predator limitation of migrant herbivores. Frank and coworkers' hyena studies are significant in showing the major impact of high female social rank on reproductive success. This study demonstrates the need to consider social interactions, not only in population modeling, but also in analyses of the maintenance of genetic diversity. Laurenson found that 53% of cheetah litters were lost to predators, mainly lions. She conveys her concern about the increased numbers of lions and other large predators, which are possibly a result of larger numbers of prey—yet another example of the interconnections that must be considered in efforts to conserve this ecosystem. Wild dogs are apparently quite sensitive to disease and other large predators. A new phenomena of rapid total pack extinction has occurred since 1985. Burrows presents a hypothesis that handling stress may lead to reactivation of latent rabies virus. Sinclair, however, views the decline as part of a 30-year process, related to increasing human populations and accelerated disease transmission, and possibly increased numbers of lions. In contrast, Waser et al. show that mongoose populations have been remarkably stable, and insensitive to annual rainfall variations. Their densities are limited by habitat, particularly safe den sites, like termitaria in tall grass with hiding cover.

Conservation biology is an extremely topical issue for the Serengeti now. Caro and Durant show how findings from animal behavior studies can contribute to more effective conservation strategies. Certainly many population processes are behaviorally influenced. Georgiades applies genetic analyses of regional wildebeest herds to determine whether the current system of wildlife preserves in East Africa are arbitrary human constructs or correspondent with natural population subunits. This type of study has been impractical until recently, but is now made possible by mitochondrial DNA isolation and amplification (PCR). This is useful for understanding how ecosystems might have been linked through animal movements in primeval times. Dobson used a disease transmission model to showed that a critical density of cattle in the susceptible phase maintains the rinderpest virus in the population. This information can be used to justify inoculation of pastoral cattle, which is expensive. Arcese et al. take a scientific approach to quantifying poaching, the factors that affect it, and efforts to stop it. Their data show exactly how increased patrol frequency and use of vehicles can increase the effectiveness of antipoaching efforts.

The effects of a large human population in proximity to the reserve were demonstrated by Cambell and Hofer, who used geographic modeling to derive a map of potential wildlife offtake. The map clearly shows areas of higher and lower potential impact, and risk. The models were tested by comparing offtake predictions to estimates generated in workshops held in 11 surrounding villages. This was a superb analysis, and I predict the spatial modeling approach will be put to greater use in the future. The areas to the east of the park, largely in the NCA, have been much neglected. With 25,000 pastoralists and 286,000 livestock grazing with native ungulates, it the only multiple land use system of its kind in East Africa, and has been for over 30 years. Perkin evaluated the effectiveness of the NCA as a conservation and development institution, drawing largely from the findings of the Ngorongoro Conservation and Development Project 1987-90. Multiple land use has been difficult to implement, as the

institutions tend to favor one extreme of land use or the other. There are pressing needs to find ways to make multiple land use systems work, but they will require interdisciplinary institutions that develop ways for multiple land users to work together. Norton-Griffiths cuts to the bottom line in assessing the economic forces. Fundamentally, there have to be real economic incentives for conservation, or it won't happen. There are huge economic incentives for the land owners to lease the land to cultivators. The Mbano et al. chapter describes the Serengeti Regional Conservation Strategy (SRCS), launched in 1985 with the resolution that an integrated approach is needed to reconcile human and conservation needs and get local communities directly involved in resource management. Thus far, the SRCS has developed sustainable resource use in local communities, facilitated the procurements of village titles to their land, and established communication channels between conservation experts and the local communities. The final chapter describes a very preliminary ecosystem simulation model constructed during a workshop. As an exercise in getting scientists to think about system-level interactions, the workshop was undoubtably a great success. But serious models involve several man-years of effort. The book jacket claims the model provides a basis for future conservation and management strategies, but this is naive, at best.

"Serengeti II" largely accomplishes its objectives. It brings us up to date on the last 20 years of research and ecosystem change, and fosters integration between pure research and applied conservation biology. The science and the integration are at the forefront. This is not just a book about the Serengeti, it makes substantial contributions to ecology and to ecosystem science. It will be an essential reference for research in conservation biology, plant-herbivore interactions, large herbivores, predators, or the human dimensions of ecological change anywhere. It is by no means a comprehensive summary of all of the research that has been conducted in the Serengeti over the last 20 years, but the references are a useful starting point. A somewhat zoological view of the ecosystem is conveyed, with disproportionate attention to animals and their effects. Studies of fundamental ecosystem processes like primary production, hydrology, nutrient cycling, and energy flows are seriously lacking. The syntheses reflects one approach to systems ecology, but there are others. All of the chapters indicate there is much work yet to be done. I recommend the book strongly, but I cannot say it that it represents *the* Serengeti. There is much more.

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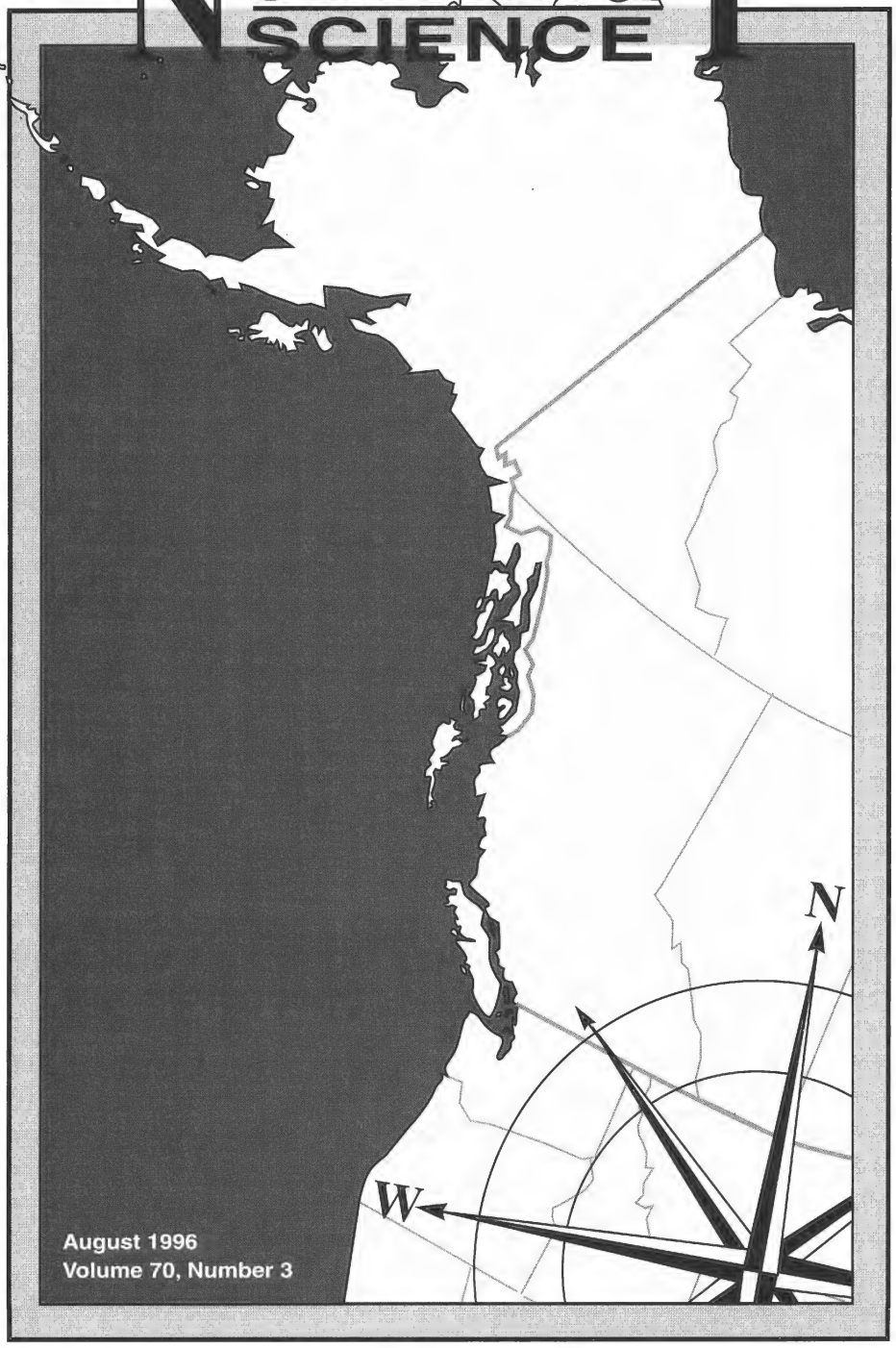

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Forest Canopies and Their Influence on Understory Vegetation in Early-Seral Stands on West Vancouver Island

Abstract

The abundance of shrubs, salal and salmonberry in particular, is a characteristic feature of the understory in old-growth, west coast forest stands. We analyzed relationships between forest canopy cover and the cover of the shrub layer, salal, salmonberry, herb layer, and moss layer using data from 157 early-seral (35 year-old) stands from west Vancouver Island having variable canopy cover, canopy species, and site quality. The analysis indicated that (i) canopy cover was influenced by canopy species and site quality, (ii) canopy cover had a strong influence on the cover of shrubs but no influence on the cover of herb and moss layers, and (iii) site quality had a moderately strong influence on the cover of salal and salmonberry and a weak influence on the cover of shrub, herb, and moss layers. As the canopy cover decreased from 95 to 5%, the shrub cover consistently increased from about 5 to 95%. The canopy cover alone was a good predictor of the cover of shrubs ($R^2 = 0.83$), salal ($R^2 = 0.72$), and salmonberry ($R^2 = 0.73$), providing the stands were stratified into poor and rich soil nutrient strata. The quantified relationships between canopy cover and the cover of shrubs, salal, and salmonberry provide a simple tool for foresters to manipulate canopy cover of early-seral stands in perhumid cool mesothermal climates for creating suitable wildlife habitats.

Introduction

Stand structure describes the characteristics of canopy (tree layer) as well as understory vegetation (shrub, herb, and moss layers) and, thus, it describes habitat suitability for animal communities (e.g., Daniel et al. 1979, Kimmins 1987, Smith 1986). The structure of a forest stand depends on a number of factors, such as, site quality (climate, soil water, and soil nutrient conditions), history of disturbance, canopy species, stand density, and stand developmental stage.

Poorly developed understory vegetation is the natural characteristic of early-seral or stem exclusion stages of stand development (Oliver 1981). When timber production is the sole management objective, there is little impetus to change the structure of early-seral stands except to control stand density while maintaining high canopy cover; thus, the stem exclusion stage may extend over a long period of time. Manipulations of both stand density and canopy cover are tools which can enable foresters to modify stand structure and to promote the development of understory vegetation. Foresters, therefore, need to know the impact of canopy manipulations on the development of understory vegetation in early-seral stands, i.e., how understory vegetation will respond to different light conditions imparted by a change in canopy cover. This knowledge may be useful in fine-tuning canopy manipulations to increase biodiversity or animal population in situations where the management goal is to maintain or improve wildlife habitats, in addition to producing wood.

The objectives of this study were (1) to characterize the forest canopy cover of seven tree species in relation to site quality and (2) to examine the possible influence of canopy cover and site quality on the cover of shrub layer, in particular salal (*Gaultheria shallon* Pursh) and salmonberry (*Rubus spectabilis* Pursh), herb layer, and moss layer by comparing estimated cover value data from 157 early-seral, west coast stands. Considering that salal (on poorer sites) and salmonberry (on richer sites) are (i) nearly absolute dominants in the shrub layer of late-seral west coast stands and (ii) important for wildlife in coastal British Columbia, our study focused on these two shrub species.

Materials and Methods

The 157 study stands were all plantations and included two B.C. Forest Service experimental

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projects established in 7 locations over a wide range of sites on south-western Vancouver Island (Omule 1987, Omule and Krumlik 1987). The experimental design was a randomized complete block with 7 tree species replicated seven times in one location and with 4 tree species replicated five times in 6 locations. Twelve stands were rejected from a total of 169 stands as they were heterogeneous in soil moisture and nutrient conditions. A replicate (stand) consisted of 81 trees planted at square spacing of 3.5 m. All stands had a similar management history the cutting of old-growth stands, slashburning, and planting one of the following: Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* (Dougl. *ex* D. Don) Lindl.), Pacific silver fir (*Abies amabilis* Dougl. *ex* Forbes), Sitka spruce (*Picea sitchensis* (Bong.) Carr.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western redcedar (*Thuja plicata* Donn *ex* D. Don), or Port-Orford-cedar (*Chamaecyparis lawsoniana* (A. Murr.) Parl). The study stands, each approximately 0.01 ha square and containing one of the 7 study species, were 35 years-old and had a wide range in canopy cover.

The study area was within the Submontane (10 to 500 m in elevation) Very Wet Maritime Coastal Western Hemlock (CWHvm1) biogeoclimatic variant, influenced by a perhumid cool mesothermal climate (Klinka et al. 1991). Site association, which is comparable to habitat type (Pfister and Arno 1980), of biogeoclimatic ecosystem classification (Pojar et al. 1987) was used as a qualitative categorical measure of site quality. Within the CWHvm1 variant, site associations were determined by identifying soil moisture regime and soil nutrient regime for each study stand, and by using the site classification for coastal British Columbia (Green and Klinka 1994). The stratification of study stands according to site associations and tree species indicated (i) the presence of site quality gradient from slightly dry to very moist sites and from very poor to very rich sites, represented by 5 site associations, (ii) occurrence of all study stands on blueberry (*Vaccinium* spp.) (SA2) sites, and (iii) occurrence of only Douglas-fir, Sitka spruce, western hemlock, and western redcedar stands on all sites (SA1 through SA5) (Table 1).

The cover of forest canopy, shrub layer, salal, salmonberry, herb layer (including ferns and herbs), and moss layer (including mosses and liverworts) in each study stand was estimated visually from 4 observation points using percent cover (the vertical crown or shoot-area projection in the stand) (Mueller-Dombois and Ellenberg 1974). Soil moisture and nutrient regimes were identified in the field using a combination of topographic and soil morphological properties and the procedure described by Green and Klinka (1994).

TABLE 1. Stratification of the study stands according to tree species and site associations identified in the study area.

Tree species	Site association				
	SA1[1]	SA2[2]	SA3[3]	SA4[4]	SA5[5]
Pacific silver fir	1	5	0	0	1
Grand fir	0	6	0	0	1
Western redcedar	2	15	2	5	9
Douglas-fir	2	15	3	5	10
Western hemlock	5	14	3	4	7
Port-Orford-cedar	0	7	0	0	0
Sitka spruce	3	15	4	5	8

[1]SA1: CwHwSalal; slightly dry and very poor, poor, and medium sites.

[2]SA2: HwBaBlueberry (*Vaccinium alaskense*, *V. ovalifolium*, and *V. parvifolium*); fresh and very poor, poor, and medium sites.

[3]SA3: BaCwFoamflower (*Tiarella trifoliata* and *T. laciniata*); fresh and rich and very rich sites.

[4]SA4: HwBaDeer fern (*Blechnum spicant*); moist and very moist and very poor, poor, and medium sites.

[5]SA5: BaCwSalmonberry; moist and very moist and rich and very rich sites.

Dry to very moist soil moisture regimes are defined by actual evapotranspiration (Et):potential evapotranspiration (Emax) ratio plus depth to water table (after Klinka et al. 1989a). Soil nutrient regimes are defined by mean mineral soil (0 - 30 cm) mineralizable-N (after Varga and Klinka, unpublished data).

Homogeneity of variance in cover data was tested using Bartlett's procedure (Zar 1984). All variables were assessed for normality using probability plots (Chambers et al. 1983). The linear model (Wilkinson et al. 1992) used for testing the effect of canopy species, site association, and their interaction with canopy cover was:

$$[1] \quad A = m + SPECIES + SA + SPECIES*SA + e$$

where *A* is canopy cover, m is the overall mean, *SPECIES* is canopy species, *SA* is site association, *SPECIES*SA* is the interaction term, and e is the error term. This test included only Douglas-fir, Sitka spruce, western hemlock, and western redcedar stands (N = 136) because they occurred on all sites (Table 1).

The linear model used for testing the effect of canopy cover, canopy species, and their interaction with the cover of understory vegetation was:

$$[2]\quad Y = m + A + SPECIES + A*SPECIES + e$$

where Y is the cover of shrub layer, salal, salmonberry, herb layer, or moss layer; m is the overall mean; A is canopy cover; *SPECIES* is tree species; $A*SPECIES$ is the interaction term; and e is the error term of the model. This test included only stands on blueberry sites (SA2) (N = 77) because all study tree species occurred on these sites (Table 1).

One-way ANOVA and Tukey's test (Zar 1984) were conducted to detect differences in the cover of forest canopy, shrub layer, salal, salmonberry, herb layer, and moss layers between study stands grouped according to site associations or tree species. Regression analyses (Draper and Smith 1966, Chatterjee and Price 1977) were used to examine relations of canopy cover and site quality to the cover shrub, layer, salal, salmonberry, herb layer, and moss layer.

Results

ANOVA by model [1] indicated that (i) the forest canopy cover varied with canopy species (p <0.001) and site quality (p <0.001) and (ii) there was interaction between canopy tree species and site quality (p <0.001). Each canopy tree species had the lowest cover on salal (SA1, slightly dry and poor) sites and the highest cover on foamflower (*Tiarella* spp.) (SA3, fresh and rich) sites (Figure 1). On foamflower sites canopy cover decreased in order from Sitka spruce to Douglas-fir to western hemlock to western redcedar.

ANOVA by model [2] indicated that on blueberry (SA2, fresh and poor to medium) sites (i) the cover of shrub layer and salmonberry was significantly related to canopy cover but not to canopy species, (ii) salal cover significantly interacted with canopy cover and canopy species, and (iii) the cover of herb and moss layers was not significantly related to the canopy cover or canopy species (Table 2).

Stratification of 157 study stands according to site associations (Table 3) and canopy species (Table 4) indicated that the mean cover of forest canopy and understory vegetation layers had a great variability within site association and canopy species. Comparisons among site associations showed that the mean canopy cover was the lowest and the shrub layer was the highest on salal sites, while the opposite was determined for foamflower sites (Table 3). The salal cover was the highest on salal sites and the lowest on foamflower and salmonberry (SA5, moist and very moist, rich and very rich) sites. The salal cover decreased and the salmonberry cover increased from poor to rich sites, but this trend appeared to be confounded with the variation in canopy cover. The cover of herb and moss layers was low, in general < 20%, and without any apparent relationship to site quality.

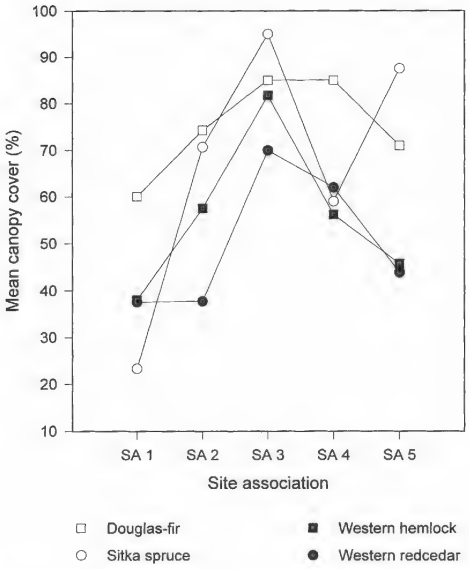

Figure 1. Mean canopy cover of early-seral Douglas-fir, Sitka spruce, western hemlock, and western redcedar stands according to site quality. Number of stands for each species and site association and abbreviations for site associations are given in Table 1.

TABLE 2. Results (p values) of ANOVA of canopy cover (A), tree species (SPECIES), and their interaction (A*SPECIES) on the cover of shrub layer, salal, salmonberry, herb layer, and moss layer, using linear model [2].

Source	Shrub layer	Salal	Salmonberry	Herb layer	Moss layer
A	0.000	0.636	0.049	0.440	0.143
SPECIES	0.475	0.022	0.154	0.610	0.069
A*SPECIES	0.351	0.015	0.247	0.643	0.109

TABLE 3. Mean, minimum, and maximum values (%) of the cover of forest canopy, shrub layer, salal, salmonberry, herb layer, and moss layer in the study stands stratified according to site associations. Abbreviations for site associations as in Table 1. Values in the same row with the same superscript are not significantly different ($p < 0.05$, Tukey's test).

	Site association				
Character	SA1 n=13	SA2 n=77	SA3 n=12	SA4 n=19	SA5 n=36
Forest canopy	37.7[c]	59.7[b]	85.0[a]	66.1[a,b]	61.5[b]
	5-65	25-95	65-95	25-95	20-95
Shrub layer	80.8[a]	51.8[a,b]	6.5[c]	43.6[b]	44.9[a,b]
	35-95	1-95	1-35	1-95	1-95
Salal	61.5[a]	23.2[b]	4.5[c]	29.2[b]	7.6[c]
	25-80	0-85	0-25	1-90	0-25
Salmonberry	3.1[c]	18.1[a,b]	1.2[c]	10.3[b]	35.6[a]
	0-10	0-75	0-5	0-65	0-90
Herb layer	10.7[b]	17.8[a,b]	11.3[b]	10.2[b]	23.8[a]
	3-45	1-30	1-40	1-40	3-70
Moss layer	9.7[a,b]	20.2[a]	3.7[b]	9.8[b]	20.1[a]
	0-50	0-60	1-15	1-40	2-40

Comparisons according to canopy species in 157 study stands indicated that the mean canopy cover was highest and that of the shrub layer was lowest in Port-Orford-cedar, Douglas-fir, and Sitka spruce stands, while the opposite was found for grand fir, Pacific silver fir, western hemlock, and western redcedar stands which had nearly consistently open canopy (canopy cover <50%) (Table 4). Regardless of species, the cover of salal and salmonberry appeared to be related to canopy cover, i.e., it was always higher in open-canopy stands and lower in closed-canopy stands. The cover of herb layer had no relationship to canopy species, but the cover of moss layer showed a weak relationship to canopy cover both being the highest in the open-canopy stands of Pacific silver fir and grand fir.

To examine relationships of canopy cover and site quality (independent variable) to the cover of shrub layer, salal, and salmonberry (dependent variables), multiple regressions were developed (Table 5). Canopy cover was a better predictor of the cover of understory vegetation than site association. The performance of the models decreased in order from the shrub to salal to salmonberry model. Canopy cover accounted for the largest proportion of the variation in the shrub cover of all models tested ($R^2 = 0.83$, Table 5, Figure 2). Multiple regressions using canopy cover and site associations as dummy variables resulted in improved performance for predicting the cover of salal (model [4]) and salmonberry (model [5]).

The models using canopy cover and site association as predictors, accounted for 58% and 43% of the variation in the cover of salal and salmonberry, respectively (Table 5). Considering the strong

TABLE 4. Mean, minimum, and maximum values (%) of the cover of forest canopy, shrub layer, salal, salmonberry, herb layer, and moss layer in the study stands stratified according to tree species. Values in the same row with the same superscript are not significantly different ($p < 0.05$, Tukey's test).

	Tree species						
Character	Pacific silver fir n=7	Grand fir n=7	Western redcedar n=33	Douglas-fir n=35	Western hemlock n=33	Port-Orford-cedar n=7	Sitka spruce n=35
Forest canopy	44.3[b]	42.1[b]	45.0[b]	75.0[a]	54.1[b]	80.7[a]	71.6[a]
	35-60	30-55	20-85	50-95	15-85	65-95	5-95
Shrub layer	65.7[a]	77.1[a]	72.0[a]	23.1[b]	61.5[a]	17.1[b]	35.1[a,b]
	40-80	55-95	10-95	1-60	1-95	5-35	1-95
Salal	23.6[a,b]	20.7[a,b]	30.7[a]	9.6[a,b]	31.9[a]	10.3[a,b]	19.5[a,b]
	5-70	5-35	1-80	0-50	2-85	2-20	0-90
Salmonberry	37.9[a]	46.4[a]	29.6[a]	10.7[b]	19.6[a,b]	4.6[b]	8.7[b]
	5-60	40-60	0-90	0-50	0-85	2-5	0-45
Herb layer	18.6[a]	21.4[a]	22.0[a]	17.0[a]	17.5[a]	11.4[a]	12.4[a]
	10-60	10-30	4-50	2-70	1-40	5-20	1-35
Moss layer	37.9[a]	35.7[a]	15.2[b]	14.7[b]	14.8[b]	17.6[a,b]	13.9[b]
	20-60	10-50	0-40	2-40	0-50	10-30	0-60

TABLE 5. Selected models for the regression of the cover of shrub layer, salal, salmonberry, herb layer, and moss layer on forest canopy cover (A) and site association (SA). All model are significant at $p < 0.05$. Abbreviations for site associations as in TABLE 1. SA1 through SA5 are dummy variables designating SAs with unit value 0 or 1. N = 157.

[3] Shrub layer (%) = 113.68 - 0.625A(%) - 0.007A²(%)
Adjusted $R^2 = 0.83$ SEE = 13.9%

[4] Salal (%) = 43.102 - 0.579A(%) + 40.245(SA1) + 14.646(SA2) + 10.578(SA3) + 24.326(SA4)
Adjusted $R^2 = 0.58$ SEE = 15.6%

[5] Salmonberry (%) = 72.825 - 0.607A(%) - 46.856(SA1) - 18.466(SA2) - 19.971(SA3) - 22.461(SA4)
Adjusted $R^2 = 0.43$ SEE = 18.2%

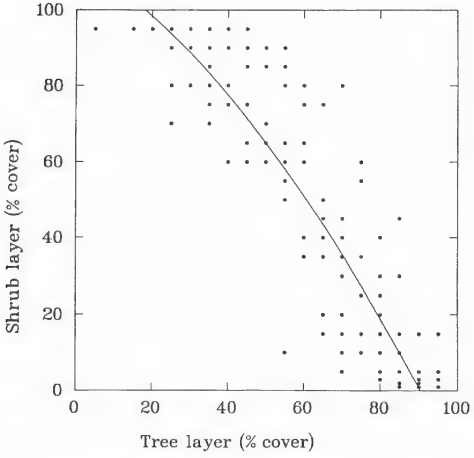

Figure 2. Scattergram and fitted regression line of shrub cover on forest canopy cover using model [3] (Table 5).

relationship between the canopy and shrub covers, a limited success of these models was not expected. Therefore, we examined the relationship between the cover of salal and salmonberry. Visual examination of the resulting scattergram suggested that these species occupy different edaphic niches. In the stands with the cover of salal >40%, salmonberry had <20% cover and was confined to special microsites, usually disturbed soils or shallow depressions. Similarly, when the cover of salmonberry was >20%, salal had <35% cover and was confined to special microsites, usually thick forest floors. The stands with a high salal cover (>40%) were those with open canopy and located typically on very poor and poor sites, less often on medium sites. The stands with a high salmonberry cover (>20%) were also those with open canopy but located typically on rich and very rich sites, less often on medium sites.

Considering a consistently low cover of salal on rich and very rich sites (SA3 and SA5), and a consistently low cover of salmonberry on very poor and poor sites (SA1, SA2, and SA4), stronger relationships between forest canopy cover and the cover of each species may be expected by deleting from the complete data set the stands on rich and very rich sites for regressing salal cover on canopy cover (n = 115), and the stands on very poor and poor sites for regressing salmonberry cover on canopy cover (n = 121). Using only canopy cover as the predictor, models [6] and [7]), each based on a presumed nutrient niche, explained >70% of the variation in the cover of salal and salmonberry (Table 6).

TABLE 6. The models for regression of salal and salmonberry on forest canopy cover (A) using for each species the data set based on its a presumed nutrient niche. Both models are significant at $p < 0.05$.

[6] Salal (%) = 94.295 - 1.038A(%)
Adjusted $R^2 = 0.72$ SEE = 14.3% n = 115

[7] Salmonberry (%) = 96.215 - 1.088A(%)
Adjusted $R^2 = 0.73$ SEE = 13.5% n = 121

Discussion

Our study of the 35 year-old, early-seral, west coast stands endorses the well-known fact that forest canopy cover, controlling below-canopy light conditions, strongly affects the cover of understory vegetation; other factors, such as site quality, pre-disturbance vegetation, and the type of disturbance, have a greater influence on the composition of understory vegetation (Daubenmire 1974, Kimmins 1987).

In the study stands, the canopy cover itself was influenced by canopy species and site quality, i.e., its influence was canopy species- and site-specific. Omule (1987), and Omule and Krumlik (1987) attributed the variation in the canopy cover to between-stand differences in site quality and between-species differences in initial mortality

and growth rates. Thus, on the nitrogen-poor, salal sites, which had the lowest canopy cover, salal must have re-established very shortly after disturbance, assumed dominance in the shrub layer, and interfered with the survival and growth of planted seedlings, especially those with a slow initial growth, as observed also by Messier and Kimmins (1990). On the nitrogen-rich, foamflower sites, early-seral vegetation was likely herbaceous and did not interfere with the survival and growth of planted seedlings, especially those with a fast initial growth.

Many authors (cited by Haeussler et al. 1990) have reported an inverse relationship between canopy cover and salal or salmonberry cover. The cover and vigour of both species in the study stands increased with decreasing canopy cover, and both species were shaded out when the canopy cover was approximately > 85%. The salal cover estimated by model [6] (Table 5) agrees with the predictions given for several canopy cover values by Messier and Kimmins (1990).

Salal and salmonberry grow best in perhumid cool mesothermal climates and both species are considered moderately shade-tolerant (e.g., Sabhasri 1961, Klinka et al. 1989a, Haeussler et al. 1990). The understory light conditions imparted by the canopy cover > 85% [corresponding approximately to <5% of above canopy light in mixed western hemlock-western redcedar stands (Messier and Kimmins 1990)] did not support salal growth in climatically comparable conditions on northern Vancouver Island (*op. cit.*). The same study and Sabhasri (1961) demonstrated that with decreasing light, salal responded with the structural changes expected in shade-intolerant species. The growth habit observed in both salal and salmonberry in the closed-canopy stands was strongly erect, loosely branched growth with a very low foliar biomass which is characteristic for shade-intolerant plants (Kimmins 1987). When the canopy cover approached 80%, we observed salal as tall as 4 m and salmonberry as tall as 6 m, which are greater heights than those given in Haeussler et al. (1990).

The difference in soil nutrient niche between salal and salmonberry in the study stands agreed with Sabhasri (1960), Franklin and Dyrness (1973), Klinka et al. (1989a), and Haeussler et al. (1990). It appears that the ecological amplitude of salal in relation to available soil nitrogen (Table 1) is within very poor, poor, and medium soil nutrient regimes, and that of salmonberry is within medium, rich and very rich soil nutrient regimes. A high salal cover (absolutely dominating) in west coast forest stands has been documented to be associated with the presence of acid Mor humus forms, often with ligneous residues; a high salmonberry cover (absolutely dominating) with the presence of less-acid, friable, Moder and Mull humus forms (Klinka et al. 1989b, 1990; Messier and Kimmins 1990). Salal and other ericaceous plants are known to tolerate acid and nitrogen-poor soils whereas salmonberry grows predominantly in association with nitrophilous species (e.g., Sabhasri 1960, Ellenberg 1974).

A generally low cover of herb and moss layers in the study stands was likely the reason for weak relationships between their cover and forest canopy cover or site quality (Table 2). This suggests that abundance of herbs in the study stands depends on some other factors, possibly shrub cover. Providing adequate light conditions (<80% of canopy cover), shrubs (either salal or salmonberry) always had higher cover than herbs, except on foamflower sites on which forest floors were shallow and friable. Reasons for low abundance of herbs and bryophytes can not be determined with certainty. Depending on site, the predominance of ericaceous species and salmonberry is the characteristic feature of old-growth stands in very wet cool mesothermal climates (Franklin and Dyrness 1973, Meidinger and Pojar 1991). We presume that this feature has been imparted to early-seral stands and that well developed and dense shrub layers have suppressed the development of the lower herb and moss layers.

The quantified relationships between canopy cover and the cover of salal and salmonberry provide a simple tool for foresters to predict how these species will respond to manipulation of the canopy in early-seral, immature stands in perhumid cool mesothermal climates. This prediction can be made by estimating canopy cover of a stand together with the soil nutrient regime of a site, i.e., estimates routinely employed in preparing silvicultural prescriptions in British Columbia. Both salal and salmonberry are important wildlife foods in coastal B.C., particularly for black-tailed deer (e.g., McTaggart-Cowan 1945, Rue 1978, Brown 1961) and black and grizzly bears (Herrero 1985). For example, if the management goal in an area

is to maintain or improve wildlife habitat in addition to producing wood, then canopy of fully stocked stands (>80% canopy cover) on fresh, moist and very moist, and rich and very rich sites (SA4 and SA5) should be opened to provide a higher understory light availability for the development of moderately shade-tolerant salmonberry. Canopy cover need not be significantly and uniformly reduced the canopy cover of 60% would result in approximately 40% salmonberry cover, which could be distributed either more or less uniformly throughout the stand or in randomly or systematically distributed gaps. Once salal or salmonberry are present on a site, further expansion is almost exclusively by vegetative means including layering and sprouting or suckering from roots and stem bases.

Conclusions

The canopy cover of early-seral west coast stands was influenced by canopy species and site quality, had a strong influence on the cover of understory shrubs, and had no influence on the cover of herb and moss layers. Site quality had a moderate influence on the cover of salal, and salmonberry. Canopy cover alone was a good predictor of shrub cover, as well as the cover of salal and salmonberry, providing stratification of stands into poor and rich soil nutrient strata. These results suggest that (i) the cover of shrub layer can be decreased or increased by increasing or decreasing canopy cover and (ii) both salal and salmonberry are moderately shade-tolerant species, each with different ecological soil nutrient amplitude.

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Spatial Variation in Productivity of Douglas-fir Stands on a Valley Floor in the Western Cascades Range, Oregon[1]

Abstract

We studied 80 to 130 yr-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands occurring on fluvial terraces and alluvial fans in the French Pete Creek valley. Our primary goals were to estimate productivity of these stands, examine relationships among landform characteristics, stand characteristics and productivity measures, and determine if productivity differs on terraces and fans. Productivity was measured as site index, leaf area index, mean annual volume increment, and periodic annual volume increment. Productivity on terraces did not differ significantly from that on fans for any measure. Spatial variability (due to plots within stands) in height ($p=0.0002$) and site index ($p=0.004$) was significantly greater within terrace stands than fan stands.

Site index of Douglas-fir stands (King 1966) on the valley floor (34 m) was greater than that estimated for surrounding uplands (31, 25 or 24 m depending on data source). In the South Fork McKenzie basin only 16-28 % of the riparian zones are on wide alluvial deposits similar to those on our French Pete valley floor study area. In part for this reason the results of this study cannot be extended directly to the nearby landscape. The current President's Plan (USDA Forest Service and USDI Bureau of Land Management 1994) calls for approximately 4,400,000 ha of riparian reserves on which timber harvest would be significantly restricted. This study indicates that when riparian reserves in the Western Cascades include wide valley floors, they may include some of the more productive stands in a basin.

Introduction

There is little published information on stocking or productivity of conifer forests in valley floors of the Pacific Northwest, and how this compares with adjacent uplands. Most studies of Pacific Northwest riparian plant communities have focused on productivity of hardwood, shrub, and herb species (e.g., Campbell and Franklin 1979), successional trends and processes (e.g., Fonda 1974, Agee 1988, Gecy 1988, Van Pelt 1991) or characterization of plant associations (Lee 1979, 1983). Some have included tree density, basal area, biomass or leaf area, but do not include productivity or make comparisons with uplands sites (e.g., Lee 1983, Gregory et al. 1991). Andrus and Froehlich (1987) estimated tree density, basal area and volume from samples of riparian vegetation along 28 streams (estimated second to third order) in the Central Coast Range of Oregon. Productivity (e.g., increment, site index) was not measured, however, and all but one stream had terraces dominated by hardwoods.

This lack of information is particularly acute because potential uses of these stands—for example, cutting for timber versus maintaining shade and logs for stream ecosystems (Gregory et al. 1991) and riparian habitat for wildlife (see papers in Raedeke 1988)—often conflict (Pedersen 1988). The President's current plan calls for about 4,400,000 ha (10,800,000 ac) of riparian reserves (Espy and Babbitt 1994). Thus estimates of the productivity of these areas, especially relative to adjacent upslope areas, are important.

The goals of this study were to document Douglas-fir productivity on the floor of a fifth-order stream valley in the western Oregon Cascades, examine relationships among stand characteristics and productivity measures, test for differences in productivity and in spatial variability of productivity between landforms (fluvial terraces and alluvial fans, terms defined in Study Area), and compare productivity of valley-floor stands with existing data for upland stands.

A fifth-order stream was chosen because they are common enough to be important, and they are typically bordered by fluvial terraces and alluvial

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fans. Smaller streams in the region often lack such landforms and are dominated by adjacent upland stands (Swanson and James 1975). Larger streams may have broader flood plains and terraces so alluvial fans are unimportant, and may be bordered by extensive stands of deciduous riparian vegetation (Hawk and Zobel 1974), complicating comparisons with adjacent coniferous stands.

Productivity measures and stand characteristics were determined on two valley-floor landforms, fluvial terraces and alluvial fans, both supporting mature Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands. These landforms differ in several characteristics, including genesis, soil and shape. The productivity measures chosen were site index, leaf area index, periodic annual volume increment, and mean annual volume increment. The stand characteristics chosen were age, mean diameter, height, tree density, Reineke's stand density index, basal area and volume.

Study Area

Research was conducted on the valley floor of French Pete Creek, a fifth-order tributary of the McKenzie River in the western portion of the Oregon Cascades Range (Figure 1). The 6-km-long study reach is located upstream from the South Fork McKenzie River and drains a watershed area of 84 km^2. Altitude of the valley-floor study area ranges from 550 m to 800 m. Mature Douglas-fir stands now dominate the forest; however, the late-successional vegetation type is the western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) series (Hemstrom et al. 1987).

French Pete Creek lies within the Three Sisters Wilderness Area and has never been logged. The preponderance of even-aged stands 80 to 130 years-old (based on ages of the oldest trees; stand origins 1856 to 1906) result from large fires in the basin during the late 19th century. Older stands are rare and occur as isolated patches. Mixed stands of alder (*Alnus rubra* Bong.), bigleaf maple (*Acer macrophyllum* Pursh), western redcedar (*Thuja plicata* Donn ex D. Don), western hemlock, and Douglas-fir occur on some terraces along with 80 to 130-yr-old Douglas-fir stands. Flood plains usually support alder. The Douglas-fir stands we studied are classified in the *Tsuga heterophylla/ Berberis nervosa, Tsuga heterophylla/ Berberis nervosa-Gaultheria shallon,* and *Tsuga heterophylla/ Gaultheria shallon* plant associations, all of which are common on well-drained, gravelly soils in the western Cascades (Hemstrom et al. 1987).

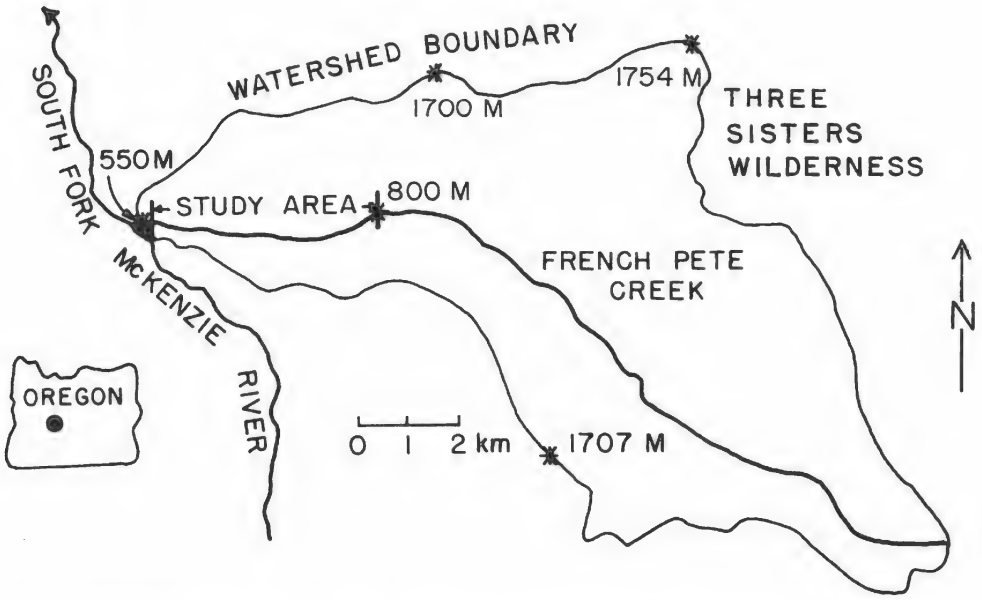

Figure 1. Location of the study area along lower French Pete Creek in the central Western Cascades in Oregon.

Four major landforms make up the French Pete Creek valley floor: the channel, active flood plain, fluvial terraces and alluvial fans. A geomorphic surface (or "surface") is a specific example of a landform, such as an individual fluvial terrace or alluvial fan (Figures 2 and 3). The width of the valley floor ranges from 9 m to 170 m in the study area. The active flood plain, and low-flow and flood channels, together occupy 14% of the valley floor, are frequently flooded, and generally do not support mature forest.

Methods

The channel, active flood plains, fluvial terraces, and alluvial fans were identified, and the entire valley floor was mapped according to these landforms (Figure 3, Table 1) as part of another study. We wanted to summarily characterize the soil environment of this valley floor, not to examine effects of soils on inter- or intra-stand variability in productivity. Soil was described in one 60-100 cm deep pit on each of three terraces and three fans chosen at random from those sampled for tree growth. Texture (hygrometer method, Day 1965), organic matter (Walkley-Black method, Nelson and Sommers 1982) and total nitrogen (micro-Kjeldahl method, Jackson 1958) of soil at the depths 0-15 cm and 15-60 cm were determined.

Stand Selection

Color infrared aerial photographs (1:8000) were used to map tree cover based on composition (hardwood, conifer, or mixed) and approximate stand age based on crown characteristics on the valley floor. The landform map was overlaid with the tree cover map.

Stands selected for vegetation sampling met the following criteria: they were (1) located on terraces or fans (since other valley floor landforms did not support Douglas-fir), (2) dominated by 80- to 130-yr-old Douglas-fir (>80% of stand basal area), and (3) located in stands large enough to contain at least five dominant or codominant Douglas-fir trees (generally 0.1 ha or larger). Old-growth stands (all with dominants much older than 130 years) and mixed stands (mixtures of broadleaved trees and conifers) were not sampled to avoid confounding landform with large differences in age and species composition. Portions of stands with pockets of canopy tree mortality apparently caused by root rot, and deeply incised channels (up to 15 m) on alluvial fans that often did not support Douglas-fir made up a small, unknown proportion of the area and were avoided.

Seventeen percent (by area) of the terraces and 86 % of the fans met these criteria (Table 1). Many terraces supported over 20 % broadleaved species and so were not sampled. Stands on 14 fans and 10 terraces were chosen for sampling.

Field Sampling

French Pete Creek field sampling, conducted in 1986 and 1989, varied in relation to the size of the geomorphic surface. On surfaces large enough to contain them, systematically located

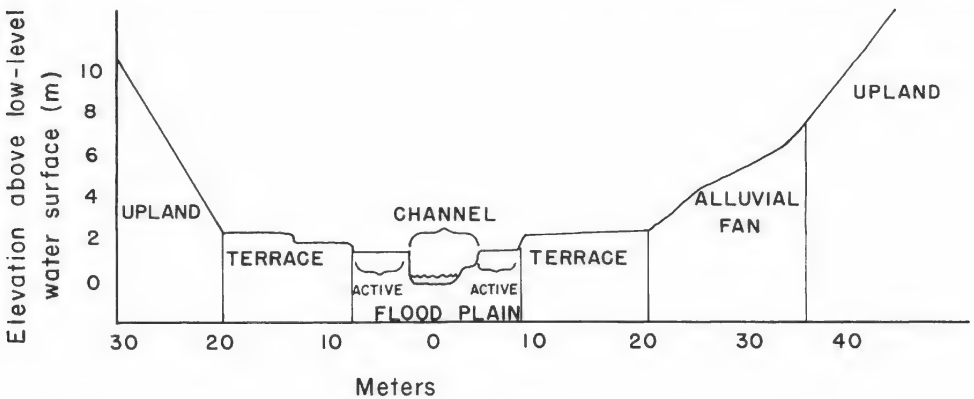

Figure 2. Diagrammatic cross-section of a hypothetical valley floor illustrating typical topographical relations of the four landforms identified in the study area. Note that alluvial fans are not necessarily paired.

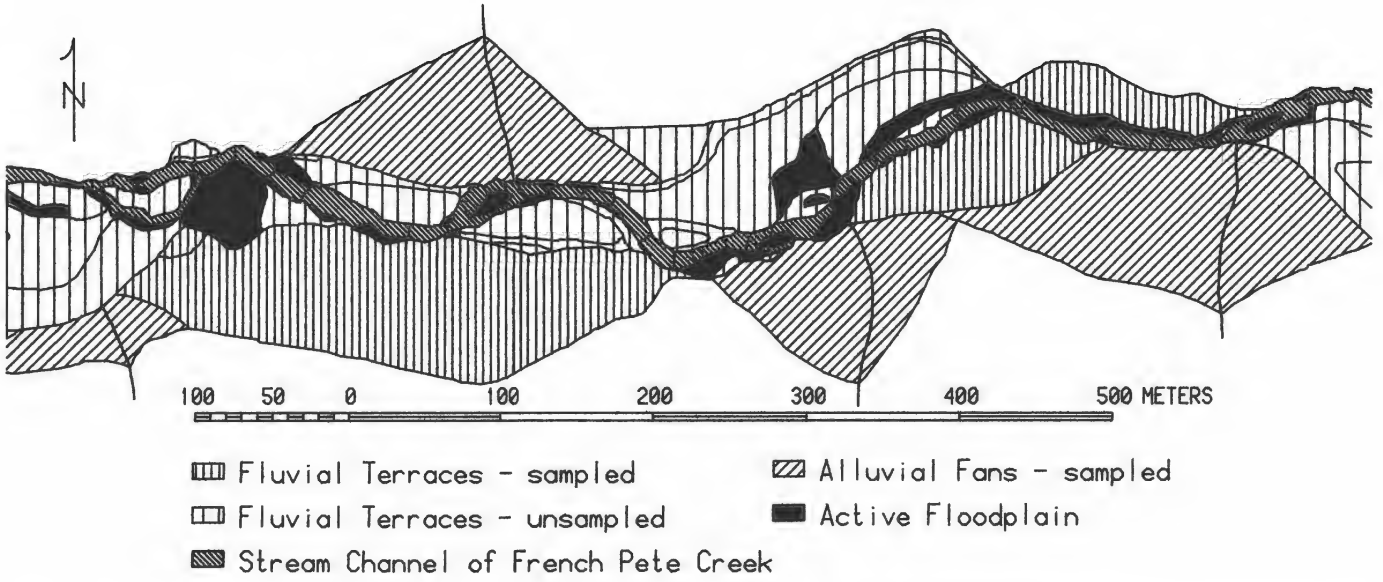
N
100 50 0 100 200 300 400 500 METERS
Fluvial Terraces - sampled
Fluvial Terraces - unsampled
Stream Channel of French Pete Creek
Alluvial Fans - sampled
Active Floodplain

Figure 3. A GIS map of a portion of the French Pete Creek study area showing the French Pete Creek stream channel, active flood plain, fluvial terraces with abandoned channels, alluvial fans and tributary streams.

TABLE 1. Cover types on the French Pete Creek valley floor, total area 41.2 ha.

Cover type	Percent of total area	
Channels	14	
Terraces:	62	
Conifer, suitable for sampling		11
Conifer, unsuitable, old-growth		12
Conifer, unsuitable, not old-growth		15
Conifer/Hardwood mix		4
Pure alder		5
Maple, maple/alder mix, other hardwood		5
Non-tree		10
Fans:	24	
Conifer, suitable for sampling		20
Conifer, unsuitable, old-growth		3
Conifer, unsuitable, not old-growth		1

variable-radius prism plots were used to estimate site index and stand productivity measures. Variable-radius plots were placed at 25 m intervals on lines spaced 20 to 30 m apart. Plots were placed 20 m from the edge of the surface to avoid the potential effects of abrupt topographic changes at surface edges.

In each plot, tree counts were obtained using a prism with a basal-area factor of 4.6 m^2/ha. Diameter-outside-bark at breast height (dbh) was recorded for tallied trees. Five (rarely 3 to 8) dominant or codominant Douglas-fir trees (herein called site index trees) were selected for increment coring (2 cores), height measurement and site index estimation. We chose only trees with no evidence of radial growth suppression to avoid problems from early competition from over topping trees and shrubs. Age at breast height (1 core only), bark thickness, sapwood thickness, and number of rings in the outer-most centimeter were recorded for these trees. A total of 56 prism plots on 5 terraces and 6 fans were sampled.

On 5 additional terraces and 8 additional fans with stands too small to contain prism plots, a minimum of 5 dominant or codominant Douglas-fir trees were selected for site index estimation.

Calculation of Productivity Measures

Several characteristics of the current stand were estimated from the field sampling. Data obtained from dominant and codominant trees were used to estimate site index at 50 yr (King 1966) for all plots and surfaces. Current volume of trees with measured height was estimated directly from dbh and height of site index trees (Walters et al. 1985). We modeled volume of these trees as: log(volume, m^3) = -8.181 + 2.146*log(DBH, cm) + 0.02900* (Plot SI, m) using standard regression procedures (n=395, r2=0.96, s.e.e.=0.11 m^3). The resulting equation was used to estimate tree volumes that were in turn used to estimate prism plot volumes using the tree-factor approach (Husch et al. 1982:220-241).

From trees with the needed measurements, equations were developed for diameter increment: DBHinc (cm/yr) = 2.9417 + 0.55930 lnDBH + 0.29084 ln(BAL+1) - 0.47469 ln(BAL+5) - 1.23306 ln (plot age) (n=249, r^2=0.166, s.e.e.= 0.3764 cm/yr) where BAL=basal area of larger trees (m^2/ha); for diameter inside bark: DIB=0.89963 DBH; and for height increment: HTinc (m/yr) = 1.1469 + 0.007398 PlotSI - 0.259045 ln(plot age) (n=344, r^2=.67, s.e.e.=0.028 m/yr).

These equations were used to estimate annual volume increment, when tree measurements of radial increment and site index were not available. Growth for each plot was expressed as periodic annual increment, and mean annual increment, and was averaged for each stand. We present net growth rates (gross growth minus mortality) because we could not estimate mortality on these temporary plots. We chose to not use a regional stand growth model (e.g., DFSIM by Curtis et al. 1981, SPS by Arney 1984) to calculate growth rates because we had much radial growth data specific to these stands.

Reineke's stand density index (SDI) was calculated according to Daniel et al. (1979). Leaf area was estimated by assigning a value of 0.54 (m^2/cm^2) to the ratio leaf area:sapwood area (Waring et al. 1982) for 337 trees with measured sapwood. For 311 trees without sapwood measurements, sapwood was estimated by a regression model of the form: log(sapwood area, cm^2) = 0.2895 + 0.7819*log(BA, cm^2) (n=337, r^2=0.62, s.e.e.=0.26 cm^2), then leaf area was estimated as above. Leaf area index (LAI) was calculated for each plot using the tree-factor approach in which values for individual trees are weighted by the tree factor to obtain an areal estimate for the plot (Husch et al. 1982:220-241).

Volumes and leaf areas of trees in lower canopy classes were probably overestimated because data

from dominants and codominants were used to build the estimating equations. The effect of this bias on reported volumes, volume growth rates, and LAI values is probably unimportant because smaller trees make up a small proportion of the total volume and leaf area. Additionally, the effect on estimates in each stand is in the same direction (overestimation), and of similar size because stand diameter distributions are all similar (not significantly different from normal, $p>0.05$ in all cases, Shapiro and Wilk 1965, and variances are not significantly different, $p>0.05$ by Bartlett's test for homogeneity of variances, Steel and Torrie 1980). For these reasons it probably has little effect on comparisons of stand means in an analysis of variance.

Statistical Analyses for French Pete Creek Data

For each of 13 measures (for all plots: average age, mean dbh and height of site index trees; additionally for prism plots: mean dbh, site index, stand density, basal area, volume, mean annual volume increment, periodic annual basal area and volume increments, stand density index and leaf area index), we tested the hypotheses that productivity of north-facing and south-facing fans was equal and that productivity of terraces and fans was equal. We used independent contrasts in an analysis of variance for a nested, unbalanced design (general linear modeling, Steel and Torrie 1980) to test each hypothesis:

	Degrees of freedom	
Source	Prism plots	Age & SI plots
Landform	2	2
N-facing fans vs. S-facing fans	1	1
Fans vs. Terraces	1	1
Stands within Landforms (experimental error)	8	21
Plots within Stands (sampling error)	45	43
Corrected total	55	66

Kendall's Tau rank correlation coefficient (Conover 1980) was used to evaluate relationships among elevation above stream, slope, age, and measures of productivity. Rank correlation was used since variance of some of the correlated variables was not uniform and some of the relationships were nonlinear.

For each measure we also tested the hypothesis that variability within north-and south-facing fans was equal using an F-ratio of the plot-within-stand variance for the north-facing fans over the plot-within-stand variance for the south-facing fans. For each measure we then tested the hypothesis that variability within fans and terraces was equal using an F-ratio of the plot-within-stand variance for the fans over the plot-within-stand variance for the terraces. Correlations between stand means and variances were negative for most measures but were not significant (all $p > 0.05$), so no correction for correlation of the variance with the mean was needed.

Comparisons with Uplands Data

We compared data for stands on the French Pete Creek Valley floor with prism plot data for stands in the surrounding central portion of the western Cascades in Oregon collected by Hemstrom et al. (1987) (eco-plot data) and by the Willamette National Forest in the 1981 National Forest Inventory (NFI data). We used eco-plot data for the South Fork McKenzie River basin that met our sampling criteria for French Pete valley floor stands, Douglas-fir basal area at least 80 % and stand age 80-130 years. We used NFI data (Willamette National Forest 1990) from stands within 48 km of French Pete Creek that were in the NFI stand types mapped for the slopes above our study reach and in the elevation range of those slopes (520-1680 m). Restricting NFI stands to those that met the Douglas-fir basal area and stand age criteria gave too few stands to make comparisons, so we were unable to calculate stocking or productivity measures. We selected dominant and codominant trees that had no damage or defect and calculated Douglas-fir site index (King 1966) for each stand.

Comparisons between French Pete valley floor and uplands stands used F-ratios in ANOVAs for unbalanced designs weighted by the number of prism plots in the stand (general linear modeling, Steel and Torrie 1980):

	Degrees of freedom	
Source	Prism plots	Age & SI plots
Data source (French Pete valley floor vs. surrounding western Cascades)	1	1
Stands within Data source (error)	25	38
Corrected total	26	39

Degrees of freedom were less for measures available only on our prism plots.

TABLE 2. Characteristics of sampled fluvial terraces and alluvial fans.

Characteristic	Fluvial terraces	Alluvial fans
Number sampled	10	14
Percent of valley floor	11% (all terraces 62%)	20% (all fans 24%)
Average width	8-83 m	23-202 m
Length	30-345 m	22-180 m
Size	<0.1-0.6 ha (1 is 2.3 ha)	0.1-1.4 ha
Origin of material	French Pete Cr.: gravel bars, abandoned channels, channel levees	Tributary streams: bedload and debris torrent material
Shape	Usually oblong, parallel French Pete Creek	Cone-shaped with apex where a tributary stream exits a side valley
Slope	<2%	8-25%
Aspect	Down stream (approx. West)	Towards main channel (10 face North, 4 face South)
Average elevation above low-flow water surface	1.5-5.4 m	3-17 m
Rock fragments[a]	Rounded, 40-70% by vol.	Angular, 40-70% by vol.
Soil texture[a]	Sandy loam to loam	Sandy loam to loam
Soil organic matter[a] 0-15 cm:	1.2-8.5%	5.7-9.0%
15-60 cm:	3.5-5.7%	2.6-4.0%
Total soil nitrogen[a] 0-15 cm:	0.03-0.10%	0.06-0.17%
51-60 cm:	0.04-0.12%	0.04-0.06%
Soil classification[ab]	Usually Typic Ustochrepts, rarely Typic Ustorthents	Usually Typic Ustochrepts

[a] Based on one pit in each of three terraces and three fans.

[b] Based on soil pits and unpublished soil temperature and climatic data from similar elevations on the H.J. Andrews Experimental Forest, 30 km north.

The above ANOVAs were performed on ranks of the data (Conover and Iman 1981) for measures with variances found to be nonuniform using Bartlett's test (Steel and Torrie 1980) or residuals found to be non-normally distributed using the Shapiro-Wilk test (Conover 1980).

Results and Discussion

Terraces and Fans

Fluvial terraces cover over 60 % of the valley floor, are oblong, and slope gently downstream (Table 2). Alluvial fans cover only 24 % of the valley floor, are cone shaped, and slope more steeply either north or south towards French Pete Creek. Terraces are made of gravel bars, abandoned channels (Figure 3), and channel levees—material that has been worked over and sorted by a fifth order stream so that rock fragments are rounded (Table 3). Fans are relatively unsorted deposits of bedload and debris flow material from first and second order streams, and rock fragments are angular. Terraces commonly support deciduous vegetation and many did not meet our sampling criteria.

Douglas-fir Stands

In general, there was a canopy of dominant and codominant Douglas-fir over fewer, comparably-aged intermediate and overtopped Douglas-fir. Younger trees of any species were very rare in the understory. Average diameter (all prism-plot trees) ranged from 43 to 65 cm, height ranged from 44 to 62 m, stand density ranged from 159 to 461 stems/ha, stand volume ranged from 638 to 1432 m^3/ha, and mean annual increment ranged from 5.9 to 12.0 m^3/ha/yr (Table 3).

Comparing north- versus south-facing fans, no productivity measures were found to be significantly different (all $p > 0.05$), though the small number of south-facing fans (n=4) limits the power of this test.

All productivity measures, stand density, stand density index, basal area and volume were greater on fans than on terraces (Table 3), however, none of these differences was significant (all $p > 0.05$).

TABLE 3. Stand characteristics and productivity measures on fluvial terraces and alluvial fans.

		Stand characteristics							Productivity measures			
Stand num	Num of plots	Age[a] (yr)	DBH (cm)	Height (m)	Stand density (stem/ha)	Stand density index[b]	Basal area (m^2/ha)	Volume (m^3/ha)	Site index[a] (m)	Leaf area index (m^2/m^2)	Mean ann. inc. (m^3/ha/yr)	Periodic ann. inc. (m^3/ha/yr)
		Fluvial terraces										
1	8	109 (6)	55 (18)	46 (12)	159 (43)	682 (32)	39 (32)	638 (34)	31 (11)	5.3 (31)	5.9 (33)	7.8 (31)
2	3	100 (10)	53 (1)	48 (22)	198 (27)	799 (29)	46 (26)	822 (45)	34 (21)	6.3 (32)	8.2 (41)	11.4 (47)
3	2	122 (8)	60 (7)	54 (7)	235 (12)	1082 (7)	69 (0)	1314 (4)	35 (4)	9.1 (7)	10.8 (3)	15.4 (1)
10	5	92 (7)	57 (6)	44 (8)	188 (17)	808 (15)	50 (18)	795 (21)	32 (7)	7.0 (19)	8.7 (22)	13.0 (24)
14	11	113 (4)	60 (6)	53 (7)	184 (31)	929 (23)	54 (23)	1009 (24)	35 (6)	6.9 (24)	8.8 (26)	12.7 (26)
All	29	107 (10)	58 (11)	48 (13)	183 (31)	837 (26)	49 (28)	872 (33)	33 (10)	6.6 (27)	8.0 (31)	11.2 (34)
		Alluvial fans										
4	10	87 (6)	53 (8)	47 (3)	219 (23)	907 (18)	51 (16)	901 (14)	36 (5)	7.0 (19)	10.4 (14)	14.0 (17)
5	7	114 (2)	57 (8)	49 (4)	210 (37)	925 (26)	55 (24)	922 (22)	33 (4)	7.0 (26)	7.9 (24)	9.8 (24)
114	2	120 (2)	58 (31)	62 (5)	250 (73)	1396 (61)	64 (30)	1335 (34)	39 (5)	7.8 (18)	11.1 (32)	14.7 (41)
116	2	120 (11)	43 (12)	55 (3)	461 (20)	2124 (2)	80 (4)	1432 (5)	35 (1)	10.9 (1)	12.0 (6)	17.5 (10)
204	2	107 (12)	60 (2)	49 (6)	241 (15)	1633 (9)	73 (9)	1261 (5)	32 (1)	9.1 (15)	11.9 (17)	15.8 (17)
205	4	112 (12)	65 (20)	55 (6)	173 (34)	1012 (24)	57 (10)	1071 (10)	35 (6)	7.2 (18)	9.8 (25)	12.4 (29)
All	17	103 (15)	55 (9)	51 (10)	232 (41)	1107 (40)	57 (22)	1030 (23)	36 (8)	7.5 (24)	10.0 (22)	13.6 (25)

Note: Values given are stand means and coefficients of variation (in parentheses).

[a]Ages and site indices (King 1966) for all terraces and all fans are based on 10 terraces and 14 fans, respectively.

[b]Stand density index in trees per hectare at reference quadratic mean DBH of 25 cm (Husch et al. 1982).

Partitioning the within-landform variance components (Hartley, Rao and LaMotte 1978) showed, for 10 of 13 response variables, more variation was due to plots within stands (60 to 94 %) than to stands within landforms. Age showed the least percentage variation within stands, only 12 %. This probably reflects common stand-initiating disturbances and regeneration lag times within stands.

Variability Within Stands

Comparing south- and north-facing fans, tree age was more variable among plots ($p = 0.005$) on south-facing fans, and was the only measure with a significant difference. On nearby uplands sites, natural regeneration commonly takes longer on drier south aspects than on north aspects (Means 1982). The higher summer evaporative demand and temperatures expected on south slopes, and lack of topographic shading by an adjacent valley wall, probably make seedling establishment more difficult, increasing the length of the regeneration period and the plot-to-plot variability in tree age.

We found plot-to-plot variability within stands to be significantly greater on terraces than on fans for height ($p = 0.0002$) and site index ($p = 0.004$) but not for other measures. Greater plot to plot differences probably reflect greater soil spatial variability on terraces than fans caused by the different processes that build these landforms. Swanson and James (1975) describe these processes for the nearby Blue River drainage. French Pete Creek creates stream channels, levees, and areas of sorted rock fragments (of different average size classes) such as gravel bars in flood plains that become terraces with abandoned channels (Figure 3) when the stream cuts to a lower level. Rounded rock fragments in terraces (Table 2) reflect fluvial reworking and sorting of deposits. In this way fluvial processes create patterns in soil parent material and micro-relief that may cause similar patterns in tree height growth rate, and therefore in site index. Our plots 25 m apart could have picked up variability caused by these patterns.

Tributary streams form the larger alluvial fans (large enough for prism plots) primarily by accretion of deposits from debris flows that overflow the incised channels, depositing relatively unsorted material (clay to large boulders), as they emerge from steep-walled side valleys. This material is not sorted by flowing water after deposition because water flow occurs on fan surfaces only during very brief debris flows and at other times is in the channels. Angular rock fragments in fans (Table 2) reflect less reworking of deposits than occurs on terraces. We thus hypothesize soils are more variable spatially on terraces than on fans. This could be tested with extensive soil sampling in another study.

On both landforms variability within stands, as indexed by coefficient of variation (CV), was relatively high (22 to 41 %) for measures such as basal area, volume, mean annual increment and

TABLE 4. Comparison of characteristics of 24 stands on the French Pete Creek valley floor with 18 eco-plot stands in the South Fork McKenzie Basin (Hemstrom et al. 1987), 13 NFI stands from within 48 km of French Pete Creek, and site quality from the Forest Survey map (Isaac 1949).

Location	Age (yr)	DBH (cm)	Stem density (stems/ha)	Stand density index[b]	Basal area (m^2/ha)	Volume m^3/ha)	Site index (m)	Mean annual increment (m^3/ha/yr)
French Pete Creek	105 (12)	57 (4)	206 (55)	779 (145)	53 (10)	779 (145)	35[a] (2)	7.4 (1.4)
McKenzie Basin	111 (11)	55 (10)	344 (150)	1031 (269)	68 (17)	1061 (274)	31 (4)	9.9 (3.0)
P-value	0.3	0.5	0.001	0.003	0.006	0.009	0.0001	0.014
NFI				972 (228)			25 (3)	
P-value				0.0505			0.0001	
Forest Survey map							24[c]	

Note: Values are means and standard deviations in parentheses.

[a] Site index (King 1966) of French Pete stands based on the tallest tree, like McKenzie Basin eco-plots.

[b] Stand density index in trees per hectare at reference quadratic mean DBH of 25 cm (Husch et al. 1982).

[c] Approximate site index calculated from mid point of site class IV on Forest Survey map (Isaac 1949) following King (1966).

LAI (Table 3) that are directly affected by stocking. Variability within stands was smaller (CV's ranged from 8 to 16), however, for stand age, height, dbh and site index, measures that are not directly affected by stocking (Table 3). The greater variability of measures such as basal area, volume, and mean annual increment makes differences in spatial variability between landforms more difficult to detect.

Comparisons with Uplands

Table 4 compares all our French Pete Creek valley floor stands with upland eco-plot stands in the surrounding South Fork Mckenzie River basin (Hemstrom et al. 1987), with upland NFI (National Forest Inventory) stands (Willamette National Forest, 1990), and with site index of the valley walls immediately above our study reach based on Forest Survey site class maps (Isaac 1949) converted to approximate site index following King (1966). Douglas-fir stands on the valley floor have significantly greater site index (34 m) than do eco-plot stands (31 m) or NFI stands (25 m) in the uplands. The valley floor stands generally have five site trees per prism plot whereas the eco-plot stands have only one and the NFI stands typically have 1-2. The French Pete valley floor stands show even greater site index (37 m) when based on the tallest tree, as might be done if only one site tree had been selected. The Forest Survey mapped the French Pete Creek basin as site class IV which corresponds to about site index 24 m (King 1966), also lower than the valley floor.

The valley floor stands, however, have lower stem density, SDI, basal area, volume, and mean annual increment than the eco-plot stands, and possibly lower SDI than the NFI stands (Table 4). Productivity comparisons with the NFI stands would not indicate site differences because some were outside the age range of the valley floor stands and not dominated by Douglas-fir, so this comparison is not considered further. The eco-plot stands were selected subjectively so chosen stands tended to have greater stocking (Hemstrom et al. 1987). We cannot conclude the apparently greater stocking on the uplands is real, though it may be. The known suppression of Douglas-fir height growth by higher stocking on low site land (Harrington and Reukema 1983, Reukema 1979) may contribute to the site index differences. We conclude, however, that the French Pete valley floor has higher site index than the surrounding uplands because we believe the magnitude of the site index differences out weighs a possible but unclear effect of stocking to reduce site index in the uplands.

Leaf area index of forests along French Pete Creek (5.3-10.9 m^2/m^2) was similar to or lower than that of subjectively selected Douglas-fir forests (7.3-12.0 m^2/m^2) sampled by Marshall and Waring (1986) in the region.

Frequent disturbances and high moisture content of riparian sites often leads to significant representation or dominance by early seral or broadleaved vegetation, as was found by Andrus and Froehlich (1987) in a study of terraces and uplands along 28 second- and third-order streams in the Oregon Coast Range. Their only valley floor stand that was comparable in age and composition to ours had conifer density, basal area, and volume very close to those of terrace 1 (Table 3). Future studies should stratify riparian zones by several of the following: width of valley floor, slope towards stream, estimated height of growing-season water table, approximate age of surface (or at a minimum, relative height of surface), relative frequency of fluvial disturbances, and species composition, and should pair adjacent riparian and upland samples.

Putting this Work in Context

The difference in productivity we found between the valley floor and uplands cannot be extrapolated directly to the surrounding landscape for two reasons. First, many riparian zone stands are less productive than those we sampled. On the French Pete Creek valley floor about 30 % of the surfaces support broad leaved, broad leaved/conifer mix, herbaceous or no vegetation, often with younger, less well-developed soils, which we did not sample. New surfaces with pure alder, shrub, herb or no vegetation (Table 1) probably would not support conifers, and surfaces supporting other pure hardwoods (Table 1) may have lower Douglas-fir site index than stands we sampled. We also did not sample riparian stands on steep and over-steepened toe slopes with thinner, less well-developed soils from which trees commonly topple into the stream, where there is no valley floor. These sites are usually closer to the stream and experience fluvial disturbances such as erosion and deposition relatively frequently.

Second, we sampled only one stream valley. In the surrounding South Fork McKenzie basin, narrower valley floors with fewer or no terraces and fans are more common than wide valley floors such as those we sampled. In this basin fans and terraces occur along approximately 28 % of the total perennial stream length when steep valley wall tributary streams are not included and along 16 % when they are (C. McCain, unpublished data, 1994).

The recent Northwest Federal Forest Plan (Espy and Babbitt 1994) calls for about 4,400,000 ha of riparian reserves in which harvest would be restricted. The reserve for our 4.4 km study reach would be 88.2 ha (41.2 ha valley floor with channel and 47.0 ha uplands) of which 25.4 ha is in nearly pure Douglas-fir stands on the valley floor, of which we sampled 12.7 ha. This work indicates that, when riparian reserves include wide valley floors, they may remove from potential harvest some of the more productive stands in a basin. This is likely to be one consequence of implementation of the recent Northwest Federal Forest Plan. This deserves further study because the magnitude of this effect cannot be assessed from this study alone.

Conclusions

Productivity of Douglas-fir stands on the valley floor of French Pete Creek is very similar on fluvial terraces and alluvial fans. It is quite variable within terraces and fans, and is high locally.

Spatial variability in productivity, as measured by tree height and site index, is greater within terraces than within fans. We hypothesize this is caused in part by greater variability in soil parent materials and topography caused by processes that create terraces.

Site index on the valley floor of French Pete Creek is greater than that of sites in the surrounding uplands. Though this result may hold for other undisturbed riparian sites with developed soils on terraces and fans, it cannot be extrapolated to recently created surfaces or stream valleys without terraces and fans, the most common riparian geomorphic setting in the South Fork McKenzie River Valley.

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Vegetation Characteristics of Alder-Dominated Riparian Buffer Strips in the Oregon Coast Range

Abstract

We examined the effects of harvesting the adjacent forest on tree regeneration, understory development, and overstory dynamics in riparian buffer strips, and compared them with undisturbed riparian communities in the western hemlock [*Tsuga heterophylla* (Raf.) Sarg.] zone of the Oregon Coast Range. All sites were dominated by red alder (*Alnus rubra* Bong.). Salmonberry (*Rubus spectabilis* Pursh) was the dominant shrub in these riparian systems and the only shrub species to increase with buffer creation. Through the chronosequence of buffers aged 0 to 32 years, little further change in overstory composition or cover was observed. Tree regeneration (seedlings younger than the overstory) was scarce. The alder-dominated riparian community appeared largely resistant to environmental changes associated with becoming buffer strips. The scarcity of tree regeneration indicates that future tree cover may be limited after alder senescence.

Introduction

In the Pacific Northwest, the extremely diverse and dynamic riparian plant communities that form a transition between aquatic and upslope systems (Beschta 1991) are important in regulating habitat quality for small mammal and amphibian species (McComb et al. 1993). They also contribute to the complexity of stream channels by introducing woody debris into the system, thereby increasing aquatic invertebrate and vertebrate habitat (Gregory et al. 1991). Such communities are a major determinant of water quality for domestic use (Anthony et al. 1987) and provide raw material for commercial wood products. To protect water quality and fish and wildlife habitat during and following logging, the state of Oregon in 1972 began to require forested bufferstrips along streams. To provide protection over the short term, these forested strips must maintain their integrity; to provide protection over the long term, the forest community must regenerate itself.

In the Oregon Coast Range, where red alder (*Alnus rubra* Bong.) is the predominant tree species in riparian areas, there have been few attempts to examine the dynamics of buffer strips. Andrus and Froelich (1988) documented the role of topography and aspect in windthrow of near-ocean buffer strips. After studying succession of Coast Range alder stands, Hibbs (1987) suggested that alder-dominated buffer strips might have an accelerated or different successional pathway from that of riparian alder stands contiguous with the adjacent, unharvested forest. Even if the successional pathway were unchanged, forest characteristics desirable for water, fish, timber and wildlife could be lost if tree cover is lost.

Studies of succession in Coast Range alder stands (Henderson 1970, Carlton 1989) have indicated that shrub dominance, especially by salmonberry (*Rubus spectabilis* Pursh), increases with time, and that tree regeneration is generally lacking (Minore and Weatherly 1994). An accelerated succession, through mechanisms like windthrow or increased rates of tree senescence could lead more rapidly to the development of this shrub-dominated community. The predominance of red alder and concern that alder-dominated forest may undergo more rapid succession (Hibbs 1987) in buffer strips make study of alder-dominated riparian communities of special interest. Study of the present vegetation structure and composition of riparian buffer strips can provide evidence of the effects of past practices and long-term riparian processes.

This study was made within the western hemlock [*Tsuga heterophylla* (Raf.) Sarg.] and Sitka spruce (*Picea sitchensis* [Bong.] Carr.) zones (Franklin and Dyrness 1973) of the Oregon Coast Range, a region in which red alder has always been a common riparian dominant (Harrington et al. 1981). Extensive logging in the early part of this century greatly increased the dominance of alder in riparian zones as well as on adjacent slopes (Hibbs et al. 1994). Our specific objective was to determine the effects on tree regeneration, understory development, and overstory harvesting

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of forests adjacent to alder-dominated riparian forests. We sampled a spectrum of buffer strips and alder-dominated riparian communities (called here "undisturbed" communities) that were next to unharvested forests. Our working hypothesis was that succession in alder-dominated buffer strips would differ from that observed in undisturbed alder communities. We used two approaches: examination of a chronosequence of buffer strips, and a comparison of buffer strips with undisturbed riparian forest.

Methods

Sampling-Site Selection

The western hemlock-Sitka spruce zones cover much of the Oregon Coast Range. Sampling sites were selected to represent the range of temperature and precipitation in these vegetation zones, and the range of geomorphology (unconstrained and constrained streams), disturbance type (undisturbed streamside vegetation; buffer strips), and buffer strip age (0 to 32 years since disturbance). General site characteristics are presented in Table 1. The overstory on all sites was composed only of red alder. A streamside terrace was present at most sites, ranging in width from 5 to 35 m, averaging 11.5 m. Stream width ranged from 1.8 to 22 m. Slopes ranged from 0° to 82°, averaging 19°. There was no significant linear relationship between stream width and buffer width.

Streamside harvest units extended several hundred meters along a stream. Sampling areas selected within these lengths had undisturbed homogeneous vegetation of variable width running a minimum of 50 m parallel to the stream. Buffer strips had a minimum of one tree every 15 m of stream length. Information was collected from 54 streamside sites: 44 buffer strips and 10 undisturbed sites. A buffer strip was defined as a riparian forest community left after upslope logging, an undisturbed site as one in which riparian and adjacent forest trees were of the same age. The buffers were of the most simple kind — a strip of trees in which there was no harvesting between the stream and a clearcut. What we call here "undisturbed" sites are stretches of riparian forest that were continuous with and the same age as the upslope forest and were selected to include the range of tree age, stand conditions, and geographic distribution represented among the sample of buffer sites.

TABLE 1. General site characteristics.

	Buffer sites (n = 44)		Undisturbed sites (n = 10)	
Variables	Range	Mean	Range	Mean
Elevation (m)	120-1200	248	80-880	369
Stream gradient (%)	0-7	2.6	1-5	2.5
Stream width (m)	1.7-22	8.6	5.7-14	9.3
Transect length (m)	5-40	18.5	25-60	45.5
Buffer age (yr)	0-32	10.5	—	—
Overstory age (yr)	17-88	43	27-102	55

Plot Establishment and Data Collection

Transects 5- to 50-m long were established perpendicular to stream flow (Figure 1). Each transect extended upslope from the stream edge, ending at the buffer edge on buffer sites, and on undisturbed sites at 60-m distance or at the edge of the alder community, whichever came first. Plots of different size were established along each transect line for tallying overstory alder trees (5 m by 15 m), shrubs (5 m by 5 m), and herbs (1 m by 1 m). Overstory and shrub plots were centered on the transect line; herb plots were 2 m distant. Overstory plots were oriented with the 5-m axis along the transect line. The first plot was located immediately adjacent to the stream; successive plots were located continuously every 5 m to the buffer or terrace edge, or until the maximum transect length was reached. When the transect extended more than five plots, succeeding plots were spaced at 10-m intervals (every other 5-m interval).

Information collected for each transect area was time since buffer creation, elevation, stream gradient, stream width, and overstory age (derived from increment cores of dominant trees). Each plot was designated as terrace, transition, slope, or hilltop. Overstory, shrub, and herb cover was estimated visually as the percentage of plot ground-area covered by each.

The overstory information collected was light, cover, and tree diameter at breast height (dbh) by species. Light was measured at three equally spaced points along the center line of the overstory plot above the shrub cover. One reading was taken in the center of the plot, the other two readings at a distance of 3 m from the plot center. Light was measured with a handheld quantum sensor and calibrated against a continuously recording sensor placed in the open.

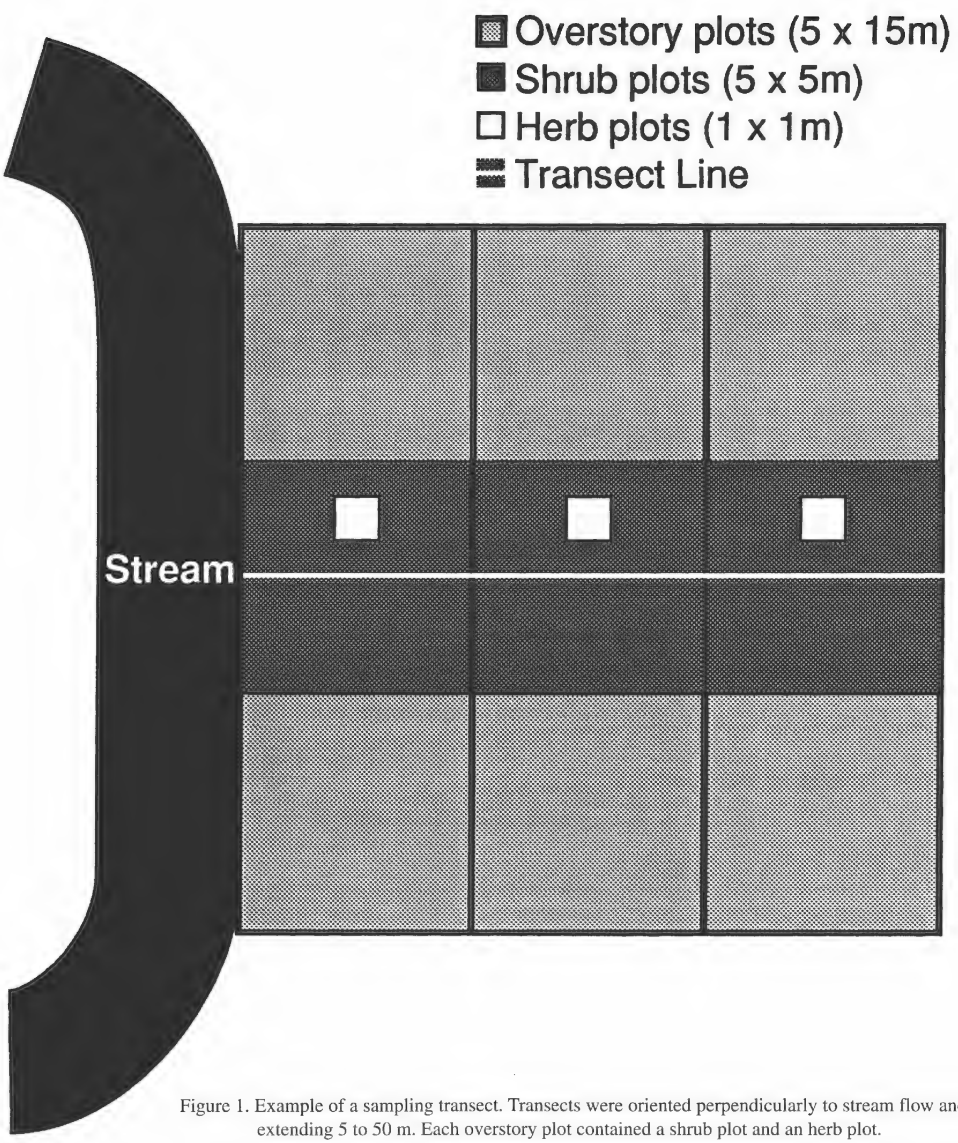

Figure 1. Example of a sampling transect. Transects were oriented perpendicularly to stream flow and extending 5 to 50 m. Each overstory plot contained a shrub plot and an herb plot.

Shrub species and cover were recorded in shrub plots and herb species and cover in herbaceous plots. Swordfern (*Polystichum munitum* [Kaulf.] Presl) cover was assessed in both shrub and herb plots because it is herbaceous but is perennially erect.

For analysis, data were partitioned into buffer and undisturbed sites, and into slope and terrace. Buffer and overstory age (in 5-year age classes) were related to vegetation characteristics. ANOVA and regression analyses were performed with SAS (SAS Institute Inc. 1987). ANOVA and means

TABLE 2. The general analysis-of-variance model for all tests and results for tree basal area, tree cover, and shrub cover. The degrees of freedom in some tests varied from the maximum shown because of missing data.

		Basal area (m^2/ha)		Overstory cover (%)		Understory cover (%)	
Effect	df	Mean square	P	Mean square	P	Mean square	P
Site type	1	216	0.63	4	0.90	6354	0.03
Replication (site type)	52	607	0.86	498	0.13	1300	0.42
Physiographic position	1	3691	0.06	1006	0.07	2717	0.14
Site type x physiographic position	1	385	0.52	1108	0.06	23	0.89
Error	18	887	—	241	—	1167	—

comparisons utilized a split-plot design (Table 2). Means comparisons were made with Fisher's Protected Test of least significant difference. Herbaceous species richness, Shannon diversity index, and species evenness were defined as in Pielou (1977) and calculated on a plot basis. Unless stated otherwise, the significance level is $p \leq 0.05$.

Results

Trees and Shrubs

Overstory cover did not differ between site types, averaging 66.9% on buffer sites and 67.9% on undisturbed sites; total basal area was also similar for both site types (35.3 and 37.5 m^2/ha, respectively). However, on buffer sites, terrace basal area and overstory cover differed from that on slopes (Table 3). We noted no more incidence of sun scald, windthrow, or stem rots in buffer than in undisturbed sites.

Total shrub cover was high on all sites and differed between buffer and undisturbed sites. Shrub cover averaged 112% on buffer strips (range 42%-236%) and 92% on undisturbed sites (range 72%-140%). In total, 22 shrub species were found on buffer sites, 17 on undisturbed sites (Table 4). On undisturbed sites, approximately 87% of the total shrub cover was salmonberry, vine maple (*Acer circinatum* Pursh), swordfern, and red elderberry (*Sambucus racemosa* L.) (Vine maple occasionally grew over 8 m tall but was always considered to be an understory species.). On buffer sites, the same four shrub species accounted for approximately 91% of total shrub cover. Salmonberry and swordfern were the most constant

TABLE 3. Differences in basal area, overstory cover, and shrub cover among site types and physiographic positions. Means in each column followed by the same letter are not significantly different ($p \geq 0.05$).

	Overstory		Shrub
Site and position	Basal area (m^2/ha)	Cover (%)	Cover (%)
Buffer terrace	52.6a	82.6a	102.1ab
Buffer slope	24.9b	54.7b	121.7a
Undisturbed terrace	41.4ab	67.6ab	79.8b
Undisturbed slope	27.2ab	68.3ab	96.2ab

TABLE 4. Mean percentage of shrub cover on undisturbed and buffer transects (± SE). The symbol "S" indicates species that were found only on slopes within the site type. No shrub species were unique to terraces.

Species	Undisturbed sites		Buffer sites	
Rubus spectabilis	35.3 (7.3)		47.3 (3.6)	
Polystichum munitum	22.7 (4.2)		19.8 (2.8)	
Acer circinatum	18.6 (4.0)		11.8 (3.3)	
Sambucus racemosa	10.5 (2.9)		12.5 (2.5)	
Corylus cornuta	3.6 (1.4)		2.8 (1.5)	S
Rubus ursinus	2.3 (1.5)		1.9 (0.6)	
Rubus parviflorus	1.1 (0.7)		6.2 (1.2)	
Ribes bracteosum	1.0 (0.8)		2.4 (0.9)	
Gaultheria shallon	< 1	S	1.1 (1.0)	S
Holodiscus discolor	< 1	S	< 1	S
Physocarpus capitatus	< 1		< 1	
Rhamnus purshiana	< 1	S	3.2 (2.0)	
Rubus laciniatus	< 1		< 1	
Vaccinium alaskaense	< 1		< 1	
Vaccinium ovatum	< 1	S	< 1	
Vaccinium parvifolium	< 1		2.1 (0.8)	
Not identified	< 1		< 1	
Ilex aquifolium	0		< 1	
Menziesia ferruginea	0		< 1	
Ribes lacustre	0		1.7 (1.4)	
Rubus procerus	0		< 1	
Salix sp.	0		< 1	

species, appearing on 100% and 91% of sites, respectively. Vine maple cover was not significantly lower on buffer sites than on undisturbed sites, but it was present on only 48% of them and was present on 90% of undisturbed sites.

Salmonberry had the highest cover of any shrub species, and only salmonberry was present on all 10 undisturbed sites. In addition, salmonberry cover was significantly higher on buffer sites, (47.3%) than on undisturbed sites (35.3%, $p = 0.08$) (Table 4).

A comparison of slopes and terraces within buffers and undisturbed sites showed that the slopes had similar shrub cover and lower overstory cover and basal area (Table 3). On buffer sites, only cover by swordfern was significantly greater on slopes (27.5%) than on terraces (10.1%). On buffer sites, 14% of shrub species were found only on slopes; on undisturbed sites, 25% (Table 4).

Overstory cover was unrelated to buffer width. Total shrub cover decreased with increasing buffer width ($p = 0.06$) and width of the undisturbed area ($p = 0.08$). Total shrub cover increased significantly with proximity to the upslope buffer edge, although the R^2 value was low (0.05). In contrast, total shrub cover had little relationship to distance from the stream edge on either buffer or undisturbed sites. Cover of individual shrub species was not significantly related to distance from the buffer edge or stream edge on buffer sites, nor was it significantly related to distance from the stream edge on undisturbed sites.

Herbaceous Diversity

Over all transects, there were 52 herbaceous species (including ferns) found on undisturbed sites and 97 on buffer sites. Twenty-two of the species found were unique to buffer sites. Species richness, evenness, and diversity did not differ between undisturbed and buffer sites (Table 5). Between terraces and slopes, no differences were found on undisturbed sites; however, evenness and diversity on buffer sites differed significantly (Table 5). In buffer strips, diversity and evenness were significantly higher on terraces than on slopes. Undisturbed sites had 12 herbaceous species found only on slopes, none found only on terraces. Buffer sites had 15 species unique to slopes and 9 unique to terraces. On individual plots, species evenness and diversity increased significantly with increasing distance from the buffer edge ($p = 0.01$ and 0.06, respectively), although the R^2 value for both was low (0.04); species richness showed no significant relationships.

Dynamics

Overstory cover was not significantly related to overstory age on either undisturbed or buffer sites, although there appeared to be developing a decreasing trend in overstory cover on undisturbed sites as overstory age increased. Total shrub cover was not significantly related to overstory tree age on either undisturbed or buffer sites. However, on buffer sites, salmonberry and hazel (*Corylus cornuta* Marsh) cover increased slightly with increasing overstory age (not to be confused with time since buffer creation; $p = 0.03$ and 0.08, respectively), and, on undisturbed sites, vine maple had a positive relationship with overstory age ($p = 0.08$).

Neither overstory cover nor basal area showed a significant linear relationship to buffer age; however, light reaching the understory decreased significantly as buffer age increased (light = 14.6 - 0.46 (age); $r^2 = 0.12$). Expressed as a percentage of open light, it decreased from 13% in new buffer strips to 6% in 20-year-old buffers.

In spite of the decrease in understory light with buffer age, buffer age seemed to have little relationship with shrub cover, which remained relatively constant over a span of 30+ years (Figure 2). Cover of individual shrub species (e.g., salmonberry)

TABLE 5. Herb indices (transect basis) for terraces and slopes on undisturbed sites and buffer sites, and the probability (P) that the two means are significantly different.

	Undisturbed sites			Buffer sites			Total plots		
Index	Terrace	Slope	P	Terrace	Slope	P	Undisturbed	Buffer	P
Richness	7.8	7.6	0.67	8.3	8.0	0.44	7.7	8.1	0.36
Evenness	0.43	0.40	0.61	0.45	0.34	0.00	0.41	0.39	0.53
Diversity	0.89	0.81	0.52	1.99	0.69	0.00	1.80	0.84	0.60

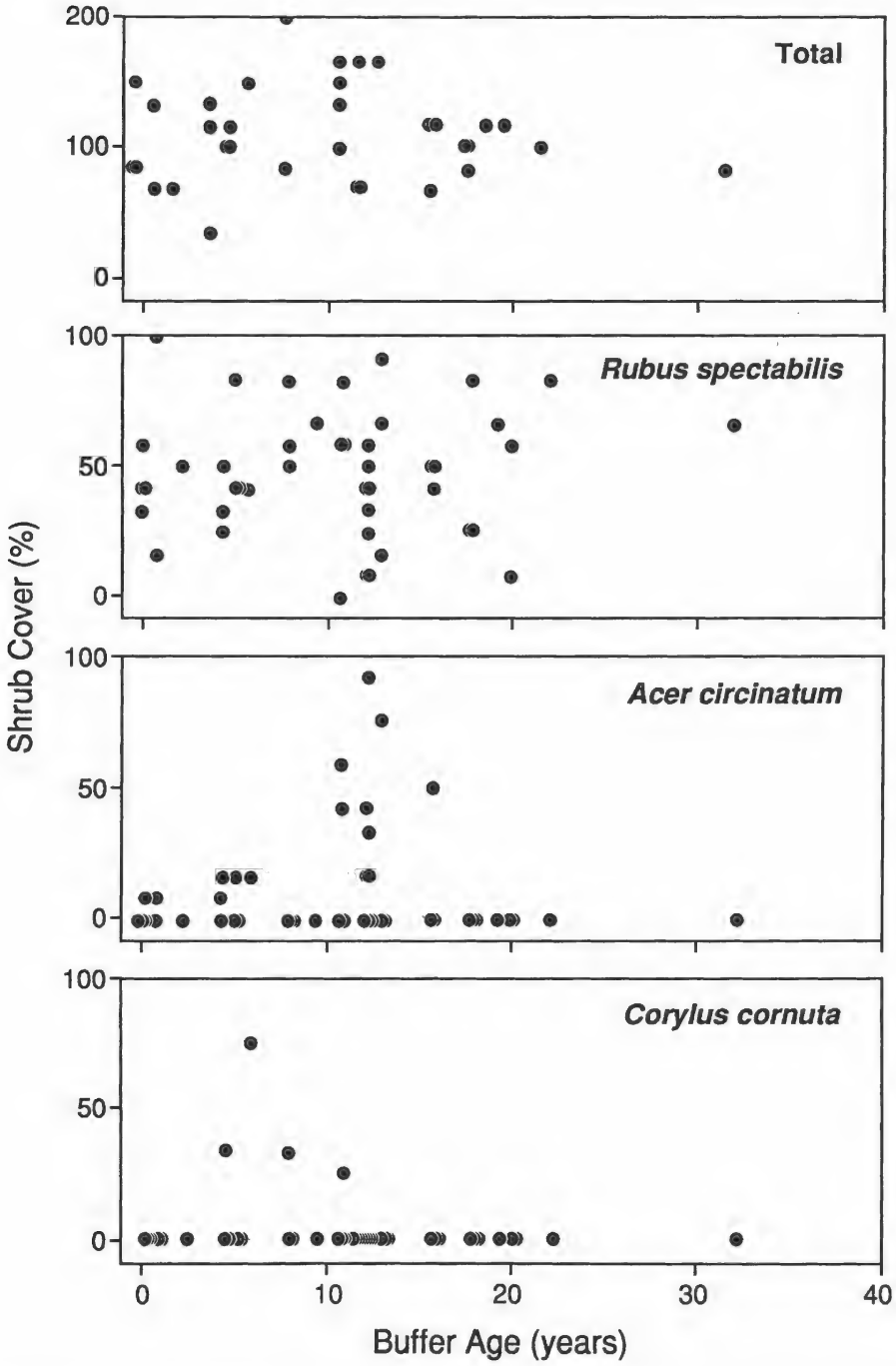

Figure 2. Change in shrub cover with buffer-strip age: a) Total shrub cover, b) salmonberry, c) vine maple, d) hazelnut.

also showed no linear relationship with buffer age, although vine maple and hazel on a small subset of transects had high values at specific times in the chronosequence (Figure 2).

Species richness, evenness, and diversity showed no significant relationship to buffer or overstory age.

Tree Regeneration

Only a small amount of tree regeneration (seedlings or trees younger than the overstory) was found. Of the 28 individuals in 1.73 ha of sample area on undisturbed and buffer sites combined, 9 were hardwood and 19 were conifer seedlings. Of the hardwood regeneration, 89% had established on mineral soil. Only 42% of conifer seedlings were found on mineral soil; others had established on rotting conifer logs (Figure 3).

Discussion

In field studies, site selection has the potential to bias results. We deliberately distributed our sites over the geographic and environmental range of the study area. Ultimately, however, selection was limited to those locations, and thus to those environmental conditions in which our sampling criteria were met: alder-dominated buffer strips or riparian areas in which there had been no partial harvesting. Did older buffer strips have a different history, (e.g., greater or lesser numbers of conifers in the now-harvested adjacent stand) than younger buffer strips? We do not know. We do

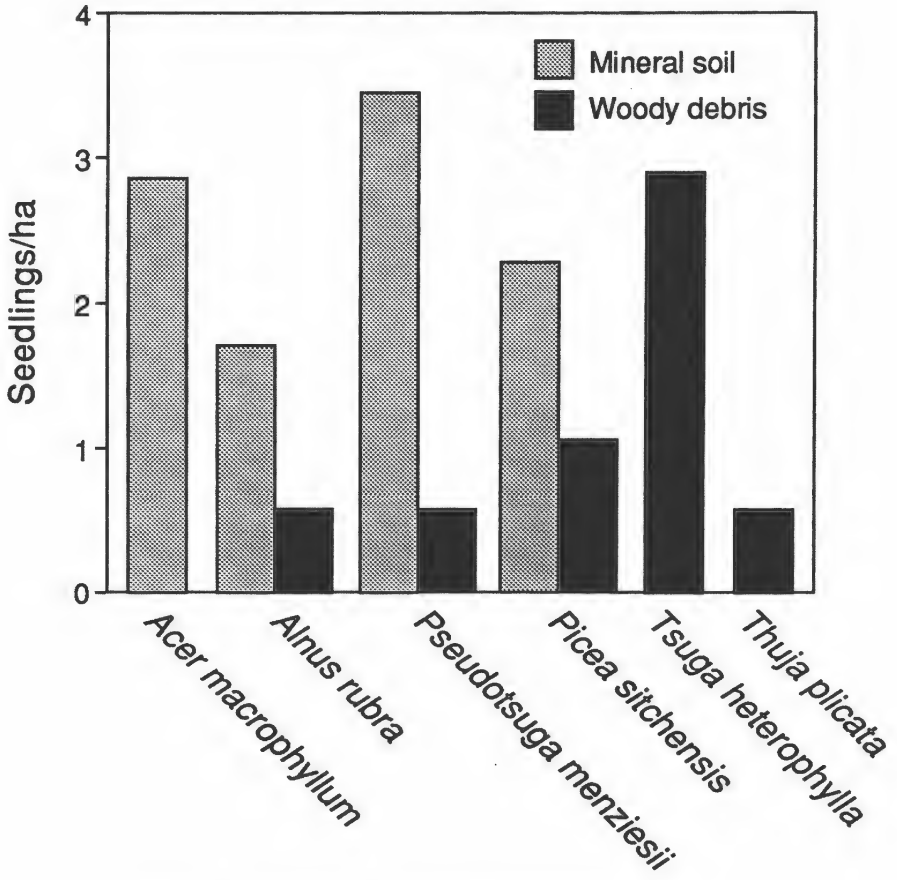

Figure 3. Tree regeneration in buffer stirps on mineral soil and woody debris.

know that all had similar post-harvest histories. Were undisturbed sites different in important ways from buffer sites? Again, there is not a definite answer. Table 1 indicates that there is a reasonable match for a number of characteristics, but one still must interpret results with caution.

We had expected to find more developmental trends in the buffer strips, inasmuch as these small pieces of forest community were suddenly placed in new environments characterized by increased side light and air movement, reduced humidity, and, perhaps, a higher water table. Such changes might be expected to affect plant growth and to change community dynamics, yet we found little evidence of this. In the overstory, we saw no more evidence of stem rot, sunscald, or windthrow than in the undisturbed sites. Overstory cover and basal area were stable through time. It seems unlikely that the similarities of buffer and undisturbed sites are due to our site-selection procedure; we simply looked for the presence of an alder overstory. We did not look at its health.

The comparison of total shrub cover on buffer and undisturbed sites showed that the creation of a buffer increased cover, which may indicate a small increase in the rate of understory development over that of undisturbed communities (Henderson 1970, Carlton 1989). There was little evidence of edge effect, only a small increase in shrub cover near buffer edges, probably lasting only until new, adjacent forest attains a height of 10 to 15 m. Although some individual species may have shown a temporary response, total understory cover was stable in buffers. Some differences in herb diversity and evenness appeared in buffers, but the differences were not great and may reflect responses to change in the shrub layer or some unmeasured site factors. The alder-dominated riparian community appears surprisingly resistant to floristic change. The general rate and pathway of succession in these communities appears fundamentally unchanged from succession on undisturbed sites.

Salmonberry has received considerable attention in recent studies of Oregon Coast Range vegetation communities (Tappeiner et al. 1991, Zasada et al. 1991). It is the most abundant shrub in the Coast Range and was the most abundant shrub in this study. Its rhizomatous regeneration habit as well as its ability to sprout vigorously after top damage allow it to colonize recently disturbed areas quickly, regenerate beneath its own cover, or re-establish itself where disturbance may have removed most salmonberry (Tappeiner et al. 1991, Zasada et al. 1991). Thickets of salmonberry often form beneath full alder canopies, greatly reducing available light in the understory. It has been speculated that total shrub cover and salmonberry cover increase in alder-dominated riparian areas as the alder canopy senesces (Newton et al. 1968, Henderson 1970, Carlton 1989). Although total shrub cover appeared to be fairly constant over time in this study, salmonberry cover in buffers increased as the overstory aged. This could indicate that total shrub cover has reached a maximum for this community type and that further successional changes will be a shift in species composition, a trend supported in undisturbed communities by the decrease in vine maple cover with overstory age.

The high shrub cover in buffer strips and the increase in salmonberry dominance may explain, in part, the scarcity of tree regeneration. Neither Henderson (1970) nor Carlton (1989) found many tree seedlings in their chronosequence studies of riparian and upslope alder stands. In alder-dominated Coast Range riparian zones, the combination of limited large woody debris (Ursitti 1991), an important regeneration substrate (Harmon and Franklin 1989, Minore and Weatherly 1994), and high shrub cover clearly limit the opportunity for natural regeneration of trees, conifer or otherwise. As these stands senesce, only a significant natural or man-made disturbance will allow reestablishment of a tree overstory.

Total shrub cover on the buffer strips (42%-236%) and undisturbed sites (72%-140%) was high compared to that in other community types in the Oregon Coast Range, where it generally ranges from 22% to 106% (Henderson 1970, Hemstrom and Logan 1986, McComb et al. 1993). The highest cover tends to be found in upslope communities. Total shrub cover in plant communities with a high salmonberry component is typically between 55% and 85% (Henderson 1970, Hemstrom and Logan 1986, McComb et al. 1993). In this study, shrub cover was similar (115%) to that in some Oregon Cascade Range communities dominated by rhododendron and salal (Hemstrom et al. 1987). These communities are generally on drier upslope sites where total shrub cover is between 54% and 118% (Hemstrom et al. 1987). Communities at higher elevations in the Cascade Mountains [Pacific silver fir (*Abies*

amabilis Dougl.) associations] can have shrub cover >150% (Hemstrom et al. 1987).

Protection of riparian ecosystem integrity from adjacent harvest activities has typically involved establishment of buffer strips. While this study shows that the overstory vegetation structure of buffer strips is similar to that of undisturbed hardwood communities, some changes appear in understory composition and cover. The initial increase in salmonberry cover after buffer creation (from 99% to 115%) and the stability of total shrub cover over time have implications for the future structure and composition of these systems. In the short term, they may be quite stable. In the future, however, diminished conifer regeneration due to present-day shrub competition and lack of woody debris could further reduce the large-wood source for stream structure and, perhaps more important, could lead to a negative cycle in which conifer regeneration is further limited by the diminishing supply of woody debris.

Artificial regeneration (planting) of conifers would require a reduction in both shrub and tree cover. Light levels above the shrub canopy were low, generally less than 10% of full sun. Shrub cover, averaging nearly 100%, would reduce ground-level light even further. Riparian regeneration studies underway in the Oregon Coast Range (Chan and Hibbs, unpublished data) are clearly showing that light levels above about 25% are needed for basic survival and minimal growth of most native conifers. In a 24-year-old alder stand, cutting 75% of the trees (69% of basal area) and 100% of the shrub cover increased light from 4% to 15% of full sun (Chan and Hibbs, unpublished data). To be successful, tree regeneration efforts in the Coast Range will require, at minimum, intensive overstory thinning or creation of moderate-size or larger canopy openings.

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Seeds, Seedlings, and Growth of Pacific Yew (*Taxus brevifolia*)

Abstract

Extensive logging damage and harvesting for taxol depleted many Pacific yew populations in western North America, and successful natural regeneration is needed to restore those populations. Field measurements of seed and seedling distribution, growth, and age indicate that yew seeds may remain dormant in the soil seed bank for more than three years. Seeds tend to be concentrated under the crowns of mature yew trees, and they can produce abundant seedlings on some clearcut-and-burned sites. Clearcutting, burning, or other major stand disturbances are not essential for seed germination and seedling survival, however; Pacific yew can also regenerate in the understory of undisturbed stands.

Introduction

Pacific yew (*Taxus brevifolia* Nutt.) occurs as an understory tree over a wide range of environments in western North America (Bolsinger and Jaramillo 1990). Many of those understory yew trees were killed during the extensive clearcutting of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) forests after World War II, and many more were destroyed when Pacific yew was harvested in large quantities from 1990 until 1993 for the anti-cancer drug taxol (USDA Forest Service and USDI Bureau of Land Management 1993a). Maintenance of the remaining yew population depends on the ability of Pacific yew to successfully reproduce and adapt to changes in its environment (USDA Forest Service and USDI Bureau of Land Management 1993b).

Unfortunately, the regeneration of Pacific yew is poorly understood. Yews often sprout from the stump, but our unpublished measurements of 900 unburned yew stumps indicate that stump-sprouting is variable and erratic. It does not occur where the stumps have been killed by broadcast burning. Seeds are borne almost every year on female yew trees (Rudolph 1974), however, and large seed crops sometimes occur. Little is known about seed-crop frequency, seed dispersal, or the soil seed bank.

Birds and rodents consume or carry off about 90% of the seeds of Japanese yew (*Taxus cuspidata* Sieb. and Zucc.) (Sakakibara 1989). The remaining 10% probably fall to the ground. The seeds of Pacific yew may be disseminated similarly. If they are, and if one assumes that seeds near a female tree were produced by that tree, the distribution of seeds that were not consumed or carried off can be determined by locating the seeds and seedlings that are present around isolated female yew trees. As the fate of local yew populations may depend on seeds and seedlings, their spatial and temporal distribution is critical. Growth rates of the resulting seedlings also will be important in the recovery of harvested populations. Measurements of large trees indicate that Pacific yew grows slowly under field conditions (Bolsinger and Jaramillo 1990, Busing and Spies 1995), and severe browsing often limits seedling growth. More growth data are needed for unbrowsed seedlings in the field.

Pacific yew successfully regenerates in old-growth forests (Busing et al. 1995), but it also may regenerate from seed soon after major disturbance. Indeed, some foresters believe that disturbance is essential to obtain yew regeneration. However, yew tends to be more abundant in northwestern old-growth than in younger stands (Spies 1991), and the species is very tolerant of shade (Minore 1979). Although tree size and age are not always correlated, all-sized diameter distributions suggest that uneven-aged, self-replacing age distributions may occur in Idaho (Crawford and Johnson 1985). It has been suggested that Pacific yew usually appears after canopy formation in the Bitterroot Canyons of Montana (McCune and Allen 1985). As it also has been suggested that population dynamics of *Taxus brevifolia* west of the Cascade crest in Oregon and Washington are similar to those of populations in Idaho and

[1] Retired

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Montana (Busing et al. 1995), uneven-aged stands and seedling establishment after canopy formation may be common throughout the range of Pacific yew.

How are Pacific yew seeds and seedlings distributed with relation to mature yew trees? Do yew seeds remain viable in the soil for long periods? How fast do the seedlings grow when not browsed? Can yew seedlings survive and grow in the absence of major disturbance? We addressed these questions by counting and measuring yew seeds and seedlings in the field to test five null hypotheses:

1. Numbers of Pacific yew seeds in the soil do not differ with distance from mature female trees, direction from those trees, or by depth in litter and soil.

2. Yew seeds in the soil do not remain viable for more than one or two years.

3. Yew seedling abundance does not differ with distance or direction from mature yew trees.

4. Unbrowsed yew seedlings do not grow rapidly (i.e. they do not average more than 10 cm of height growth per year).

5. Seedlings of Pacific yew do not occur in the absence of major, stand-replacing disturbance.

We tested these hypotheses on Pacific yews growing in a relatively small portion of the Cascade Range of western Oregon. Therefore, rejecting or failing to reject a hypothesis does not necessarily imply rejection or failure throughout the range of Pacific yew. Rejected hypotheses provide information on local yew regeneration characteristics or species potentials, however, and they should be considered when managing or studying yew elsewhere.

Methods

Hypothesis #1 (uniform seed distribution) was tested by locating isolated, mature female yew trees in the central Cascade Range of western Oregon. After extensive searching in the Willamette National Forest (Lat. 43° 54' to 44° 24' N. and Long. 122° to 122° 15' E.), only five isolated female trees could be found. They were selected without regard to size or environment. Each bore fruit or female flower buds, and each was at least 33 m from another female tree. All were on level topography with little slash, brush, or debris at elevations between 700 and 1,100 m. Diameter, height, and crown dimensions of each isolated tree were recorded. We collected soil samples from the north, south, east, and west sides of each tree at distances of 0, 1, 2, 4, 8, 12, and 16 m from the bole. At each distance, the litter and soil in a 25 x 25 cm square was removed from three depths (0-5 cm, 6-10 cm, and 11-15 cm) and placed in plastic bags. We sifted each soil sample in the field through a series of progressively finer soil sieves. Intact yew seeds were trapped in No. 7 (2.80 mm) and No. 8 (2.36 mm) sieves, separated from debris of similar size, and saved in labelled plastic bags.

Beginning at the bole and working outward in each direction, we carefully sifted soil from all three depths at 0, 1, 2, and 4 m. If the two lowest depths were without seeds at 4 m from the bole, only the 0-5 cm sample was sifted at more distant sampling points. All depths were assumed to be without yew seeds when seeds were absent from the surface layer at these more distant points. Wherever seeds were found in the 0-5 cm depth, at any distance, soil samples from the other two depths also were sifted. Intact seeds obtained from each soil sample were taken to the laboratory, counted, and floated in water to separate hollow seeds (which floated) from sound seeds (which sank). Samples of both were cut to verify this test. Numbers of intact seeds at each location and depth were compared in a split-split plot analysis of variance in which directions were the main plots, distances were sub plots, and depths were sub-sub plots (Snedecor and Cochran 1967). Tree diameters, tree heights, and crown volumes were compared to total numbers of seeds in simple regression analyses.

Hypotheses #2, #3, and #4 (seed viability, seedling distribution, and seedling growth) were tested in a fenced Douglas-fir plantation established in a clearcut- and broadcast-burned area that supported many yew trees before it was logged. The clearcut area was located in the Cascade Range of western Oregon (Lat. 44° 02' N., Long. 122° 20' E., elevation 800 m). After it was broadcast-burned in June 1986, only dead yew stumps, seeds in the soil, and a few seedlings that escaped the fire remained. Abundant western redcedar (*Thuja plicata* Donn.) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) in nearby uncut stands indicated a moist, summer-wet, mesothermal environment (Klinka et al. 1989). Unusually abundant

Pacific yew stumps and seedlings in the clearcut area also suggested particularly favorable conditions for Pacific yew. We measured the abundance and distribution of yew seedlings that were present around six isolated yew stumps in August, 1993 by establishing six circular, 200 m^2 plots in the fenced plantation. Each plot had a radius of 7.98 m, and each was centered on a yew stump that was at least 16 m from other yew stumps. Only the most isolated yew stumps that were surrounded by seedlings were used as plot centers, but yew stump density in the clearcut unit precluded greater plot isolation. Each of the plot-center stumps was assumed to be the remnant of a female tree that produced the yew seedlings nearby. Because of the clumped manner in which seedlings surrounded the isolated stumps and the abundance of both stumps and seedlings elsewhere in the plantation, we also assumed that seedlings from off-site seed sources were absent. All of the yew seedlings in each plot were numbered, located by azimuth and distance from the central stump, and measured to determine total height. They were then cut at the soil surface, labelled, and aged by counting annual rings in the laboratory. We dug only a few seedlings, but none showed any evidence of sprouting, and age at the soil surface was recorded as total age.

Hypothesis #2 (seed viability limited to one or two years) was tested by counting the number of seedlings in each of the eight age classes that corresponded to the eight growing seasons between seed-source destruction and seedling harvest. Assuming that none of the seedlings came from off-site seed sources (a reasonable assumption because of the clumped distribution of seedlings around isolated stumps), seedlings less than five years old would provide support for rejecting this hypothesis.

Hypothesis #3 (uniform seedling distribution) was evaluated by dividing each of the circular 200 m^2 plots into halves. Three halving directions were tested in separate analyses: uphill versus downhill, north versus south, and east versus west. In each test, the semicircular halves were further divided into equal-area sub plots that occupied areas with inner and outer radii of 0 to 4.00, 4.00 to 5.64, 5.65 to 6.91, and 6.92 to 7.98 m. Seedling densities (the number of seedlings per square meter) were compared with split-plot analyses of variance in which directions (uphill versus downhill, north versus south, or east versus west) were the main plots and distances were the sub plots.

Hypothesis #4 (yew seedling growth) was assessed by determining mean seedling height by age class on the six plantation plots. To assure that all growth was protected by fencing and not influenced by browsing, only seedlings established during the eight growing seasons since June, 1986, were used.

Hypothesis #5 (relation of yew regeneration to major disturbance) was evaluated by sampling seven unfenced Douglas-fir stands with summer-wet, mesothermal environments in the Cascade Range of western Oregon. In selecting those stands we only sought to demonstrate the ability or inability of Pacific yew to regenerate between stand-replacing disturbances. Therefore, only stands that contained yew seedlings < 1 m tall in the understory were chosen, and a wide range of overstory stand ages was selected. The first ten understory yew seedlings were measured and cut at the soil surface as they were encountered in each stand. Overstory stand ages were estimated from Douglas-fir increment cores, and yew seedling ages were determined by ring counts in the laboratory. Large differences between Douglas-fir overstory and Pacific yew understory ages in one or more stands would provide grounds for rejecting hypothesis #5, because no major, stand-replacing disturbance occurred after the measured overstory trees became established.

Results and Discussion

Hypothesis #1 (seed distribution) was tested on female trees that varied in size and form. The smallest was 10 cm in diameter at breast height. It was 3.4 m tall with an average crown width of 2.9 m and a crown volume of 6 m^3. The largest tree was 41 cm in diameter, 9.9 m tall, 8.8 m wide, and had a crown volume of 174 m^3. The number of intact seeds found under and around the five mother trees varied among trees, but regression analyses indicated that seed abundance was not significantly ($P < 0.05$) related to the measured tree size and crown characteristics . Direction from the parent tree also was unrelated to seed abundance, because the average number of seeds per m^2 of soil did not differ significantly ($P < 0.05$) on the north, south, east, or west (Table 1). Significantly more yew seeds were found in the soil immediately next to the bole (0 distance) than

TABLE 1. Average number of yew seeds per square meter found in the soil around five female trees—by distance from the bole, depth, and direction.[1]

Distance (m) and Depth (cm)	North	South	East	West	All Directions[3]	All Depths and Directions[3]
0						169.9
0-5	441.6 ± 260.8[2]	441.6 ± 350.5	489.6 ± 359.6	284.8 ± 146.6	414.4 ± 135.3	
6-10	147.2 ± 100.5	60.8 ± 49.2	76.8 ± 65.5	28.8 ± 13.8	78.4 ± 31.5	
11-15	12.8 ± 9.3	12.8 ± 9.3	32.0 ± 24.8	9.6 ± 9.6	16.8 ± 7.1	
1						64.5
0-5	70.4 ± 23.5	294.4 ± 115.4	102.4 ± 38.7	153.6 ± 95.7	155.2 ± 41.0	
6-10	6.4 ± 6.4	60.8 ± 27.9	3.2 ± 3.2	35.2 ± 12.8	26.4 ± 9.0	
11-15	0	44.8 ± 23.4	0	3.2 ± 3.2	12.0 ± 7.0	
2						18.7
0-5	44.8 ± 19.8	51.2 ± 27.0	48.0 ± 16.0	51.2 ± 18.5	48.8 ± 9.5	
6-10	3.2 ± 3.2	16.0 ± 12.4	0	6.4 ± 6.4	6.4 ± 3.6	
11-15	0	3.2 ± 3.2	0	0	0.8 ± 0.8	
4						2.7
0-5	3.2 ± 3.2	3.2 ± 3.2	0	25.6 ± 21.8	8.0 ± 5.6	
6-10	0	0	0	0	0	
11-15	0	0	0	0	0	
8						0.8
0-5	0	9.6 ± 9.6	0	0	2.4 ± 2.4	
6-10	0	0	0	0	0	
11-15	0	0	0	0	0	
All distances[3]						
0-5	112.0 ± 58.8	160.0 ± 76.6	128.0 ± 76.1	103.0 ± 38.8	125.8	
6-10	31.4 ± 21.9	27.5 ± 12.0	16.0 ± 13.5	14.1 ± 4.7	22.2	
11-15	2.6 ± 2.0	12.2 ± 5.8	6.4 ± 5.2	2.6 ± 2.0	5.9	
All distances and depths	48.6	66.6	50.1	39.9		

[1]Based on 25 cm x 25 cm samples at each distance and depth in each direction. All seeds were intact and apparently undamaged, but cutting tests showed that only four percent were sound. None were found at 12 and 16 m.

[2]Standard error of the mean

[3]Differences among distances and differences among depths are significant ($P<0.01$). Differences among directions are not.

farther out, however, and there were more seeds at 1 m than at 4 or 8 m from the bole ($P < 0.01$). All seeds found at distances of 4 m or more from the bole occurred in the surface 0-5 cm. Only a few were found at the 8-m distance, and none occurred at 12 or 16 m from the bole. More than 80% of the seeds found were near the surface (0-5 cm) when all distances were considered (Table 1). There was a significant ($P < 0.01$) interaction between distance and depth, because seed numbers declined with increasing distance from the bole more rapidly at 0-5 cm than at the 6-10 or 11-15 cm depths. Floating and cutting tests showed only 4% of the intact yew seeds to be sound. Nevertheless, hypothesis #1 was rejected with respect to distance and depth, because almost all of the seeds present around the five isolated yew trees were under parent tree crowns and near the surface. It was not rejected with respect to direction, for our isolated trees showed no significant ($P < 0.05$) differences in seed distribution on the north, south, east, and west.

Hypothesis #2 (seed viability) seedling ages showed that yew seeds germinated over a 7-year period in the clearcut, broadcast-burned, and fenced Douglas-fir plantation. The age distribution of 613

yew seedlings resembled a normal curve (Fig. 1). A few older seedlings must have escaped the broadcast burning, but our data indicate that 59% of the seeds that germinated successfully after the broadcast burn did so during the following three growing seasons. The remaining 41% became established after more than three years. Indeed, 16% of the seedlings present in 1993 originated from seeds that did not germinate until at least the fifth growing season after logging and burning destroyed all local seed sources except the soil seed bank. Assuming that those late-germinating seeds were not transported to the site from non-local seed sources, we rejected hypothesis #2. Yew seeds probably remain viable for more than two years.

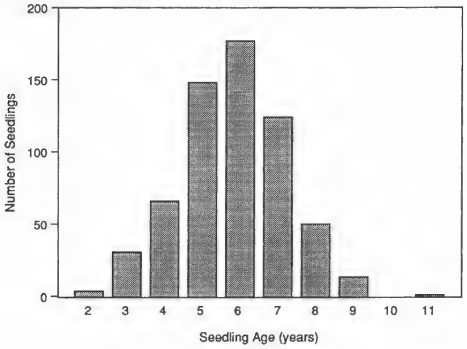

Figure 1. Age distribution of 613 yew seedlings measured during the eighth growing season after the broadcast-burning and fencing of a clearcut area.

Hypothesis #3 (seedling distribution) seedlings were not uniformly distributed among our sample plots. Numbers of seedlings around the six isolated yew stumps in the fenced Douglas-fir plantation ranged from 19 to 175 per 200 m^2 plot. Slopes varied from 45% to 66%, but there was no significant ($P < 0.05$) difference when seedling densities uphill and downhill from the parent stump were compared. There were significantly ($P < 0.05$) more seedlings west of the stumps (azimuths of 180° to 359°) than there were east of the stumps (azimuths of 0° to 179°), but the north-south difference was not significant. Seedling densities were highest near the stumps and lowest farther away (Table 2). Hypothesis #3 was rejected; seedling abundance differs with distance and direction from mature yew trees.

Hypothesis #4 (seedling growth) seedlings demonstrated a consistent growth trend with little

TABLE 2. Average number of yew seedlings per square meter, by distance and direction from six parent tree stumps.[1]

	----------Direction---------		
Distance (m)	West (180°-359°)	East (0°-179°)	All Directions[3]
< 4.00	1.0 ± 0.1[2]	0.5 ± 0.2	1.5 a
4.00 - 5.64	0.5 ± 0.2	0.4 ± 0.1	0.8 b
5.65 - 6.91	0.6 ± 0.2	0.5 ± 0.1	1.1 ab
6.92 - 7.98	0.3 ± 0.1	0.3 ± 0.2	0.6 b
All distances[3]	2.4 a	1.7 b	

[1]Each of the stumps was >16 m from any other yew stump in the clearcut-and-burned, fenced area surveyed. Equal-area, 25 m^2 plots were used.

[2]Standard error of the mean. n = 6.

[3]Means in the same row or column that are followed by different letters are significantly different ($P < 0.05$).

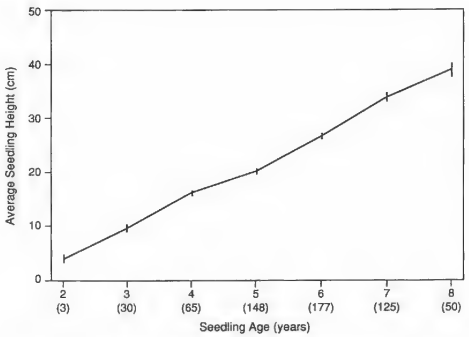

Figure 2. Average heights of unbrowsed yew seedlings, by age class. Numbers in parentheses indicate the number of seedlings measured in each age class. Vertical lines represent standard errors of the means.

variation when average height was plotted against average age for each age class (Fig. 2). All 598 seedlings were inside the fence and unbrowsed. They maintained a height-growth rate of about 6.5 cm per year during the six years from age 2 until age 8. That does not equal the arbitrary 10 cm threshold that we used to define rapid growth, and hypothesis #4 was not rejected.

Hypothesis #5 (regeneration and disturbance) stands had overstory Douglas-fir trees from 15 to more than 200 years old (Table 3). Average understory yew seedling ages ranged from 4 to 12 years in those stands, and none of the seedlings were more than 50 years old. Most were probably affected by browsing, and seedling height

TABLE 3. Overstory age, yew seedling ages, and yew seedling heights from seven Douglas-fir stands in western Oregon.[1]

Stand	Overstory Age (yrs.)[2]	Range in Seedling Age (yrs.)	Average Seedling Age (yrs.)	Range in Seedling Height (cm)	Average Seedling Height (cm)
A	15	2-6	4.1 ± 0.5[3]	7-30	14.1 ± 2.5
B	15	5-14	8.6 ± 1.0	21-88	35.8 ± 6.3
C	20	5-14	9.1 ± 1.0	20-46	36.0 ± 2.8
D	20	3-11	6.6 ± 0.9	16-37	22.7 ± 2.1
E	35	8-15	11.7 ± 0.9	25-115	62.6 ± 9.5
F	140	1-43	12.2 ± 4.1	4-70	30.6 ± 8.2
G	>200	2-14	6.9 ± 1.3	5-71	34.3 ± 6.7

[1]Ten yew seedlings were measured in each stand.

[2]From increment-borer cores

[3]Standard error of the mean. n = 10.

was not directly related to either seedling age or overstory age. The five stands with young (<50 years) Douglas-firs in their overstories had young yew seedlings in their understories that indicated seedling establishment during the stand replacement that occurred after major disturbance. Two stands with older (>100 years) Douglas-firs also had young yew seedlings in their understories, however, and those young seedlings did not require a stand-replacing disturbance to become established. Hypothesis #5 was rejected; seedlings of Pacific yew can become established in the absence of major, stand-replacing disturbance.

We did not study long-distance seed dispersal, but our data provide general, qualitative information about local yew seed and seedling distribution, and they illustrate characteristics of the species that probably are important in most yew environments under most stand history scenarios. For example, most yew seeds not consumed by birds or mammals tend to drop from the crown and remain nearby with little local dispersal. Many apparently fall straight to the ground and remain there. They are concentrated beneath the parent crown and are equally distributed on all sides of the bole. This may result in frequent regeneration within family clusters and could account for the high levels of yew inbreeding reported by El-Kassaby and Yanchuk (1994). Where abundant Pacific yew is the dominant forest species, however, yew seed dispersal is random (Crawford and Johnson 1985).

Yew seeds may be capable of surviving for more than three years in the soil seed bank, because some seeds germinated to provide a new crop of yew seedlings seven years after other local seed sources (live trees) had been destroyed. The seedlings around a mature yew tree tend to be most abundant near the bole or stump, but they may not be equally distributed on all sides of that tree. Differences in seed germination and seedling mortality associated with aspect, shading, and solar radiation may be responsible.

Clearcutting and broadcast burning do not always destroy yew seeds in the soil seed bank, and burned yew stumps may be surrounded by seedlings if conditions are favorable for seed germination and seedling survival. Those seed-bank seedlings may be critical in preserving local gene pools. They also enable Pacific yew to use the abundant light and favorable growing conditions created by major, stand-removing disturbances; thus maintaining local yew populations. Clearcutting, burning, or other major stand disturbances are not essential for seed germination and seedling survival, however; yew can also regenerate naturally in the understory of old stands, without major disturbance.

Acknowledgements

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Germination of Idaho Fescue and Cheatgrass Seeds from Coexisting Populations

Abstract

We investigated Idaho fescue (*Festuca idahoensis* Elmer) and cheatgrass (*Bromus tectorum* L.) seed germination to see if persistence of Idaho fescue on cheatgrass-invaded central Oregon rangelands could be explained by rapid germination or stress tolerance. Rapid germination would increase chances of Idaho fescue seedlings successfully competing with cheatgrass seedlings, which germinate very quickly following autumn precipitation. Stress tolerance might enable Idaho fescue seedlings to establish despite soil moisture use by cheatgrass. We germinated seeds of Idaho fescue and cheatgrass collected from four sites in central Oregon where the species coexist. Seeds were germinated at three levels of water stress (0, -0.5, and -1.0 MPa, adjusted using polyethylene glycol) in controlled-environment chambers programmed to simulate autumn temperatures and photoperiods. Germination of Idaho fescue was slower, and fewer seeds germinated, compared with cheatgrass. Fewer Idaho fescue seeds germinated at -1 MPa compared to 0 and -0.5 MPa, but water stress had little effect on percent germination of cheatgrass seeds. Cheatgrass seeds began germinating in 1-2 days at 0 MPa and 2-5 days at -1 MPa compared to 4-5.5 days at 0 MPa and 9.5-14 days at -1 MPa for Idaho fescue. Median response times of both species increased with increasing water stress, but were consistently greater in Idaho fescue. For both species, increasing water stress had the least effect under conditions simulating September compared to August and October simulations. Differences among populations existed in both species, but were not biologically significant in Idaho fescue populations. Persistence of Idaho fescue populations on cheatgrass-invaded central Oregon rangelands is not due to a germination response that minimizes differences in time of emergence between the two species or tolerance of moisture stress.

Introduction

Persistence of Idaho fescue (*Festuca idahoensis* Elmer) on degraded central Oregon rangelands is puzzling, because native bunchgrasses are often out-competed by introduced species (Melgoza et al. 1990; Melgoza and Nowak 1991; Eissenstat and Caldwell 1988; Harris 1967) and because Idaho fescue is a preferred forage of ungulates (Vavra and Sneva 1978; Dragt and Havstad 1987). Heavy grazing by domestic livestock following settlement (Strong 1940; Galbraith and Anderson 1971) extirpated Idaho fescue from some central Oregon sites (Driscoll 1964). Recolonization of these sites is unlikely because Idaho fescue seed dispersal is largely limited to the immediate vicinity of the maternal plant (see Marlette and Anderson 1986) and native perennial grasses are scarce in soil seed banks (Koniak and Everett 1982; Hassan and West 1986; Rice 1989). Even with removal of heavy grazing, cheatgrass (*Bromus tectorum* L.) may prevent recruitment of Idaho fescue because the alien is well-dispersed, dominates the seed bank, and grows rapidly. Cheatgrass likely inhibits recruitment in Idaho fescue populations by depleting soil moisture and thereby decreasing the probability of survival of neighboring seedlings (see Melgoza et al. 1990; Harris 1967).

Idaho fescue seeds mature in early August, dispersal is prompt, and at least part of the seed crop is not dormant (Goodwin et al. 1995). Reproductive effort varies with abiotic conditions in Idaho fescue, but seeds are produced in all but the driest years (pers. obs.). We reasoned that persistence of Idaho fescue populations required seedling recruitment. For recruitment to occur, Idaho fescue seedlings would have to successfully compete with co-occurring cheatgrass seedlings following germination. Because cheatgrass is a winter annual, and because time of emergence strongly influences the outcome of competitive interactions (Samuel and DePuit 1987; Weiner 1985; Ross and Harper 1972), we reasoned that autumn cohorts of Idaho fescue seedlings had the best chance of successfully competing with cheatgrass. If Idaho fescue persistence on cheatgrass-invaded sites is due, at least in part, to competitive ability of Idaho fescue seedlings, then seeds from degraded-site populations should show attributes during germination that are similar to cheatgrass. We predicted that Idaho fescue seeds collected from populations persisting on

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cheatgrass-invaded sites would begin germinating as soon as, germinate as rapidly as, attain equivalent germination percentages to, and be no more sensitive to moisture stress than cheatgrass seeds. Alternatively, recruitment may be due to tolerance of moisture stress in Idaho fescue. If such tolerance were evident during germination, Idaho fescue germination percentages should remain relatively constant over a range of moisture stress while cheatgrass percentages drop.

Materials and Methods

Above-normal precipitation in 1989 resulted in good seed set by Idaho fescue and cheatgrass, and seeds of both species were collected shortly before seed shatter in central Oregon (Fig. 1). The collection sites are climatically similar, lie between 970 and 1185 m, and are all north or northwest facing. Soils at the four sites are xeric mollisols. Surface horizons have similar pH (6.6 to 6.9), but soil phosphorus and nitrogen differ. The McCoin site is relatively nitrogen rich (4.6 and 1.7 mg/kg of NH_4-N and NO_3-N, respectively) compared to the other sites (averaging 3.7 mg/kg NH_4-N and 0.6 mg/kg NO_3-N). Soil phosphorus varies from a low of 17.5 mg/kg at McCoin to 22.5 mg/kg at Combs Flat (see Goodwin 1993 for greater detail). The collection sites have been subject to long-term grazing (see Strong 1940; Galbraith and Anderson 1971).

Seeds of both species were mechanically threshed using a Forsberg® Mill and filled seeds were separated from chaff using a seed blower. Within a species, blower settings were held constant. Mean seed mass did not differ within the Idaho fescue or cheatgrass populations following processing. Processing was completed in September 1989, and processed seeds were stored in paper bags at room temperature. Germination was tested in 1991, two years after seed collection.

We tested seed germination using completely randomized experiments run in programmable (Hoffman® SG-30) germinators. Each experiment simulated temperatures and photoperiod for one of three months of late summer/autumn (August, September, and October). The temperatures used, their duration, and photoperiods were based on means calculated from 40 year records of climate for Redmond, Prineville, and Madras in central Oregon (Anon. 1983, 1981-1989). To better mimic soil surface temperatures, which we lacked and which are more extreme than air temperatures, we used mean maximum and minimum air temperatures for each month. In the August experiment, temperatures and photoperiod were 29°C (18 hours)/6°C (6 hours) with lights on for 14 hours during the warm period. Conditions were 23°C (17 hours)/4°C (7 hours) with 12.5 hours of light in the September experiment, and 18°C (16 hours)/1°C (8 hours) with 11 hours of light in the October experiment. The August and September experiments were run concurrently in two germinators; the October experiment was run after completion of the August experiment made a germinator available. Because each temperature plus light simulation was run only once in a single germinator, these treatments were not replicated and hence cannot be tested statistically.

We employed three levels of water stress in our experiments. Distilled water was used for a low stress treatment (0 MPa). Osmotic potentials were adjusted to -0.5 and -1.0 MPa using polyethylene glycol 8,000 (PEG) (Michel and Kaufmann 1973; Michel 1983) to impose greater moisture stress on germinating seeds. Manipulating osmotic potential equaled manipulating water potential because the germination substrate was saturated and seeds were not immersed. Because a germination substrate can absorb water while excluding larger PEG molecules, concentrating the solution, the ratio of solution to substrate should be 12 or greater to maintain desired potentials (Hardegree and Emmerich 1990). Our ratio of solution (50 ml) to substrate mass (3.5 g) was 14.3. Fungicides were not applied because the reaction between PEG and other solutes is synergistic (Michel 1983).

We used an electronic seed counter to count samples of 50 seeds from each of the Idaho fescue and cheatgrass seed populations. Seed samples were randomly assigned to treatments, and replicates were randomly assigned to shelves in germinators. In all experiments, 50 seeds in a germination box constituted an experimental unit. Seeds were evenly distributed on moistened cellulose (Kimpak®) in transparent acrylic boxes (11 x 11 x 3 cm). High humidity was maintained by placing germination boxes in transparent plastic bags. Germination was defined as emergence of a seminal root or coleoptile 5 mm in length. We examined boxes for seed germination daily, and germinated seeds were removed. Each experiment ran for 30 days. After seeds began germinating,

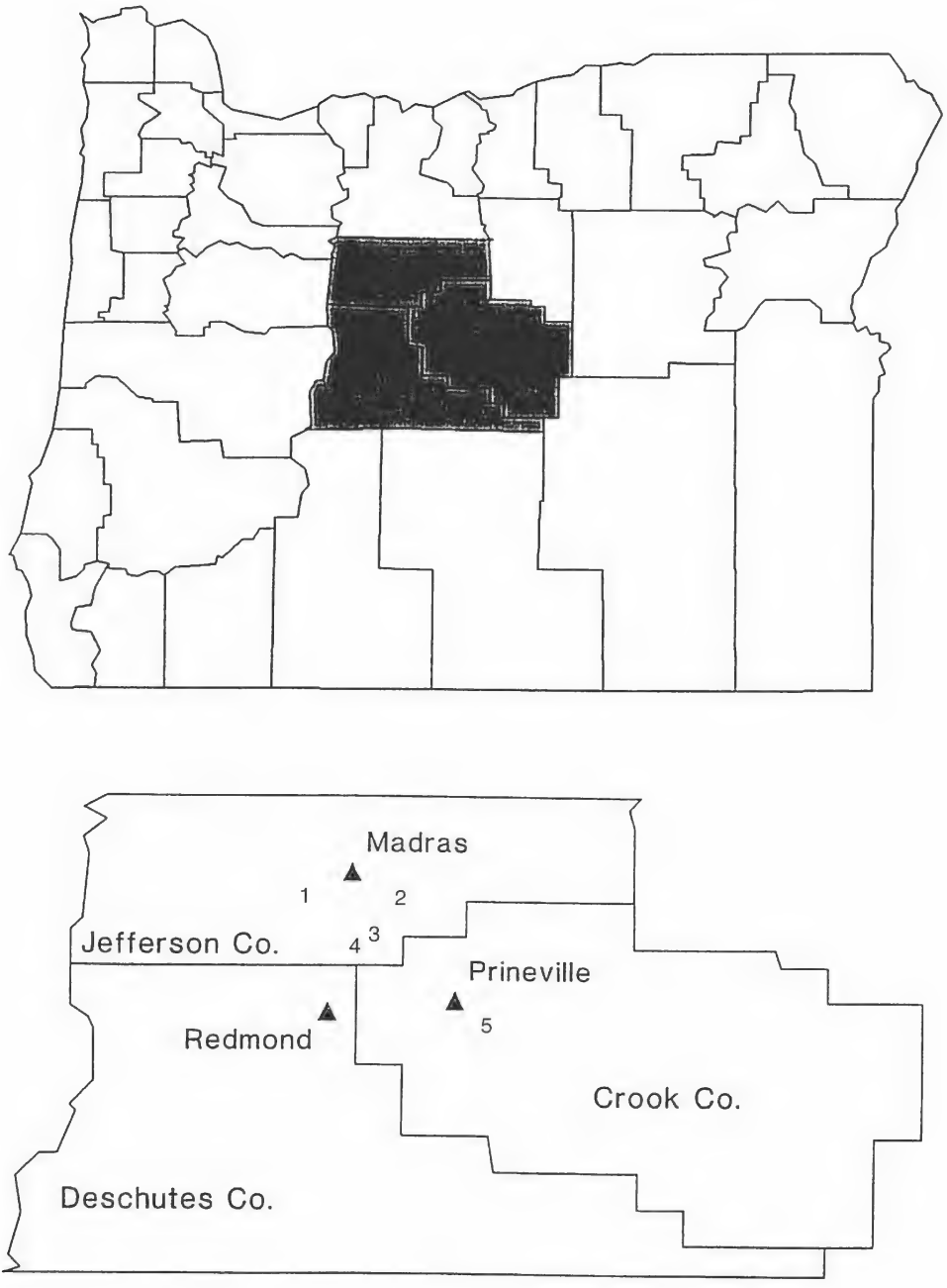

Figure 1. Map of Oregon and the locations of the Redmond, Prineville, and Madras climate stations and the seed collection sites: 1) Blanchard; 2) Lone Pine; 3) McCoin; and 4) Combs Flat. The distance between sites 1 and 4 is less than 50 km.

germination within a replicate was considered to have ceased if seven consecutive days passed with no additional germination.

We measured or calculated percent germination, days to the start of germination, median response time, and Maguire's (1962) coefficient of the rate of germination (CRG). Median response times were calculated from the number of seeds that actually germinated in each replicate: time required for 50% of these seeds to germinate equaled median response time. The CRG values were calculated as:

$$CRG = \sum_{i=1}^{30} \left[\frac{N_i}{T_i} \right]$$

where N_i is the number of seeds germinating on the i^{th} day and T_i is the i^{th} day from sowing.

Data were analyzed using Number Cruncher Statistical System™ (Hintze 1990). Within an experiment, results for each population were examined for normality, outliers, and homogeneity of variance. Idaho fescue response variables passed normality, outlier, and homogeneity of variance tests. Two cheatgrass variables, days to germination and CRG, were log (base e) transformed to satisfy ANOVA assumptions; other variables did not require transformation. Data were analyzed using two factor (population and water potential) ANOVA. A separate ANOVA was run for each response variable. If an F-test proved significant (a=0.05), Fisher's Protected LSD was used to separate means. To allow comparison with Idaho fescue, untransformed means for the transformed cheatgrass variables are reported. However, tests of differences using these variables used transformed data.

Results

Idaho Fescue

Percent germination of Idaho fescue seeds was primarily a function of water potential (August: F=75.63, p<0.001; September: F=32.41, p<0.001; October: F=30.78, p<0.001). The same percentage of seeds germinated at 0 and -0.5 MPa in the August (Fig.2) and September (Fig. 3) experiments, but fewer germinated at -1 MPa. In the October experiment, each drop in water potential resulted in fewer seeds germinating (Fig. 4). Differences among populations proved significant only under October conditions (F=3.58, p=0.023). The McCoin and Lone Pine populations had the highest germination percentages (about 84.5%), Combs Flat the lowest (77.8%), and Blanchard (82%) did not differ from either group. The delay before a seed germinated was greatly influenced by water potential (August: F=141.05, p<0.001; September: F=104.85, p<0.001; October: F=338.68, p<0.001). As water stress increased, more time passed before seeds began germinating (Figures 2, 3 & 4). Germination began most quickly in the September experiment at each level of water stress. Differences among populations were significant only in the October experiment (F=3.74, p=0.02). McCoin seeds, requiring 9.9 days, were slower to begin germinating than Blanchard seeds, which took 8.7 days, given cool temperatures and short day lengths.

Median response times did not differ between populations in the three experiments, but did vary with water potential (August: F=230.63, p<0.001; September: F=178.89, p<0.001; October: F= 779.20, p<0.001). The inhibitory effect of increasing water stress on Idaho fescue seed germination was much less evident in the September experiment (Fig. 3) compared to the August (Fig. 2) and October (Fig.4) experiments. Water potential was the only factor affecting CRG of Idaho fescue seeds in the September experiment (F=510.36, p<0.001). At 0 MPa, CRG equaled 6.59. The CRG dropped to 3.90 at -0.5 MPa and to 2.22 at -1 MPa. In both the August (F=3.32, p=0.010) and October (F=4.49, p=0.002) experiments, the interaction of population x water potential was significant. The CRGs declined rapidly with increasing water stress in both experiments (Table 1). Differences among populations varied between the two experiments and with water potential.

Cheatgrass

The interactions of population x water potential affected percent germination of cheatgrass seeds in the August (F=2.36, p=0.050) and October (F=3.94, p=0.004) experiments. In both, percent germination was greatest in the McCoin population, followed by Blanchard, with Lone Pine and Combs Flat lagging far behind (Table 2). Water potential had little influence on percent germination.

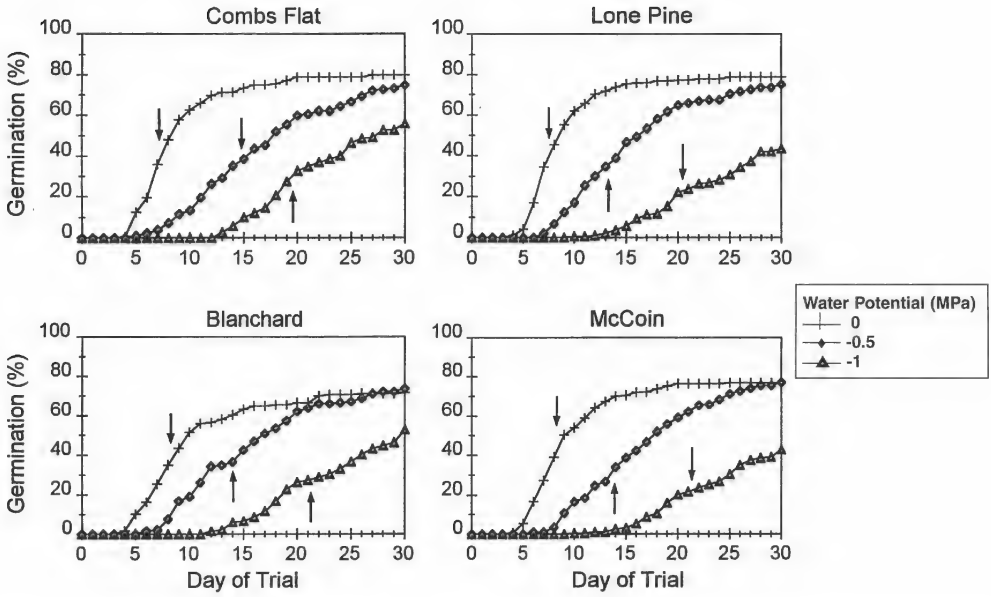

Figure 2. Idaho fescue seed germination under conditions simulating August in central Oregon for four populations. Arrows mark the median response time for each treatment.

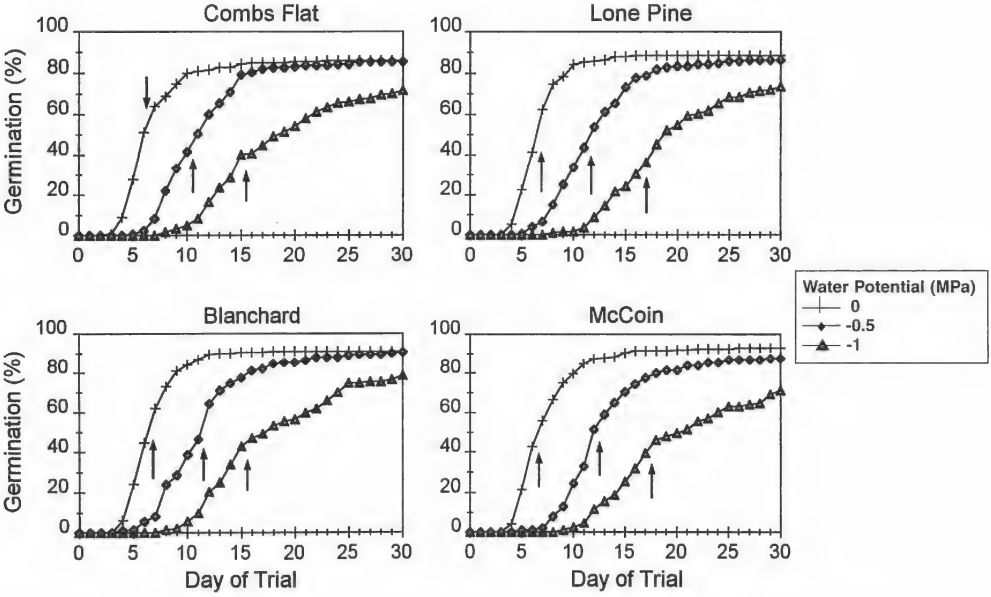

Figure 3. Idaho fescue seed germination under conditions simulating September in central Oregon for four populations. Arrows as in Fig. 2.

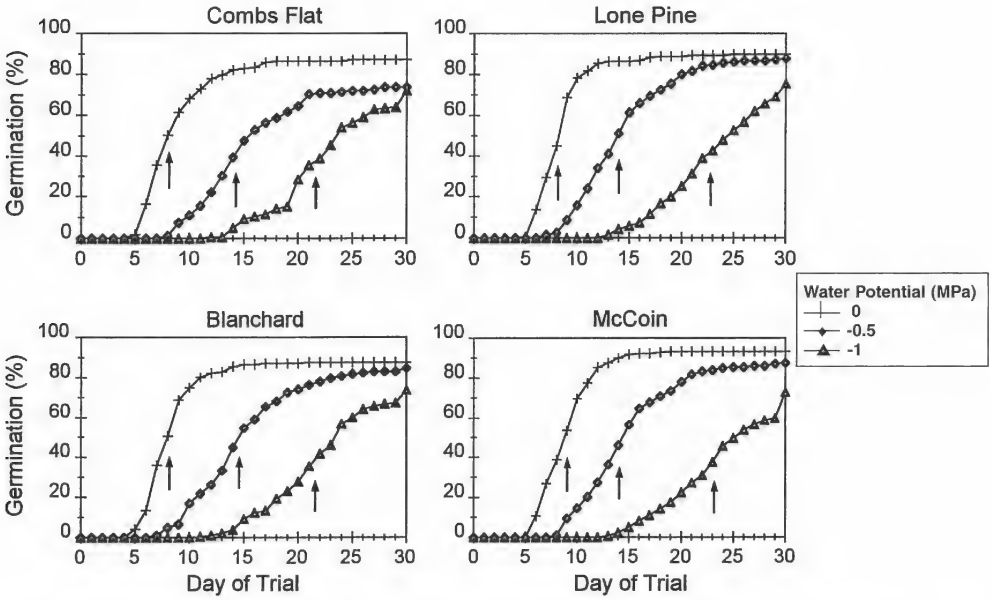

Figure 4. Idaho fescue seed germination under conditions simulating October in central Oregon for four populations. Arrows as in Fig. 2.

In the September experiment, percent germination of cheatgrass seeds was influenced by both population ($F=275.71$, $p<0.001$) and water potential ($F=9.09$, $p<0.001$). The McCoin seed population averaged 91% germination, and Blanchard 81%. The Lone Pine and Combs Flat populations had much poorer germination with 58% and 41%, respectively. Seed germination was largely insensitive to water stress. Only at -1.0 MPa did fewer seeds germinate (64%) compared to water potentials of 0.0 and -0.5 MPa (71% and 68%, respectively). Cheatgrass seed germination commenced very soon after placing seeds on moistened substrate. Only water potential affected days to

TABLE 1. Two-way interaction means for the coefficient of the rate of germination (CRG) of Idaho fescue seeds in the August and October experiments.

Ψ	Population			
(MPA)	Combs Flat	Lone Pine	Blanchard	McCoin
August				
0	4.75Aa	4.80 Aa	3.86Ba	4.34ABa
-0.5	2.46Ab	2.76Ab	2.62Ab	2.80Ab
-1.0	1.36Ac	1.05Bc	1.27ABc	1.00Bc
October				
0	4.37Ba	5.43Aa	5.31Aa	5.12Aa
-0.5	2.30Bb	3.27Ab	2.86Ab	3.09Ab
-1.0	1.57Ac	1.68Ac	1.67Ac	1.52Ac

Within an experiment, different uppercase letters indicate significant differences within a row; different lowercase letters indicate significant differences within a column (Fisher's LSD, $\alpha=0.05$). August SE=0.1683. October SE=0.1199.

TABLE 2. Two-way interaction means for percent germination of cheatgrass seeds in the August and October experiments.

Ψ	Population			
(MPA)	Combs Flat	Lone Pine	Blanchard	McCoin
August				
0	42.71Aa	55.59Ba	84.26Ca	89.76Ca
-0.5	54.71Ab	56.64Aa	84.28Ba	85.06Ba
-0.1	44.46Aab	61.25Ba	79.12Ca	90.96Da
October				
0	46.49Aa	57.97Ba	76.96Ca	96.56Da
-0.5	45.01Aa	57.89Ba	82.73Cab	95.44Da
-1.0	44.57Aa	53.47Ba	88.93Cb	83.31Cb

Within an experiment, different uppercase letters indicate significant differences within a row; different lowercase letters indicate significant differences within a column (Fisher's LSD, $\alpha=0.05$). August SE=3.0342. October SE=2.7526.

germination in the three experiments (August: $F=79.91$, $p<0.001$; September: $F=32.55$, $p<0.001$; October: $F=513.82$, $p<0.001$). Seeds began germinating after 1-2 days when water potential was 0.0 MPa, 1-3 days at -0.5 MPa, and 2-5 days at -1.0 MPa. Germination started quickest under September conditions and was slowest under October conditions. Median response times consistently increased with increasing water stress. In the August and September experiments, median response time varied with both population (August: $F=5.03$, $p=0.005$; September: $F=3.29$, $p=0.032$) and water potential (August: $F=390.99$, $p<0.001$; September: $F=120.60$, $p<0.001$). Median response time increased from 2.2 to 4.0 to 10.6 days as water potential was lowered from 0 to -0.5 to -1.0 MPa in the August experiment (Fig. 5). The McCoin population had a significantly lower median response time than Combs Flat under August conditions; Lone Pine and Blanchard median response times did not differ from those of the other populations. The inhibitory effect of water stress was reduced under conditions simulating September, with median response times of 2.1, 3.1, and 4.8 days at 0, -0.5, and -1.0 MPa, respectively (Fig. 6). Only the Combs Flat seed population was slower than the others under September conditions. In the October experiment, only water potential proved significant ($F=54.98$, $p<0.001$). Under October conditions, median response times were 3.3, 4.8, and 7.8 days at the three levels of water stress (Fig. 7). Interactions of water potential and population influenced CRG of cheatgrass seeds in the August ($F=2.36$, $p=0.051$), September ($F=2.43$, $p=0.045$) and October ($F=5.47$, $p<0.001$) experiments. Increasing water stress resulted in lower CRGs, except for the Combs Flat population in the August experiment (Table 3). The McCoin and Blanchard populations had the highest CRG's in all three experiments, and Combs Flat the lowest. The CRGs were higher at all levels of water stress in the September experiment, and were lowest under October conditions.

Discussion

Germination characteristics can affect the density and dominance of species in a grassland (Olff

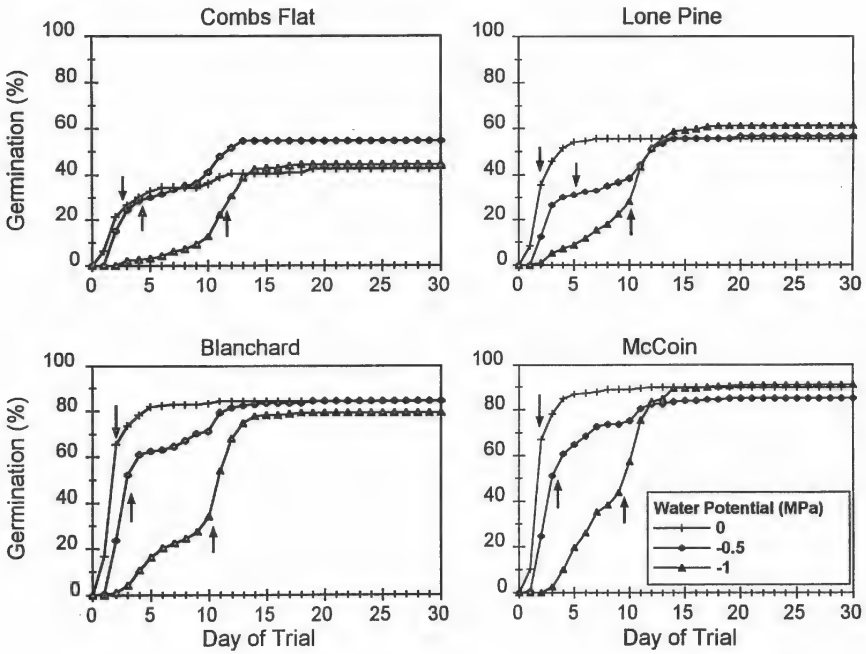

Figure 5. Cheatgrass seed germination under conditions simulating August in central Oregon for four populations. Arrows as in Fig. 2.

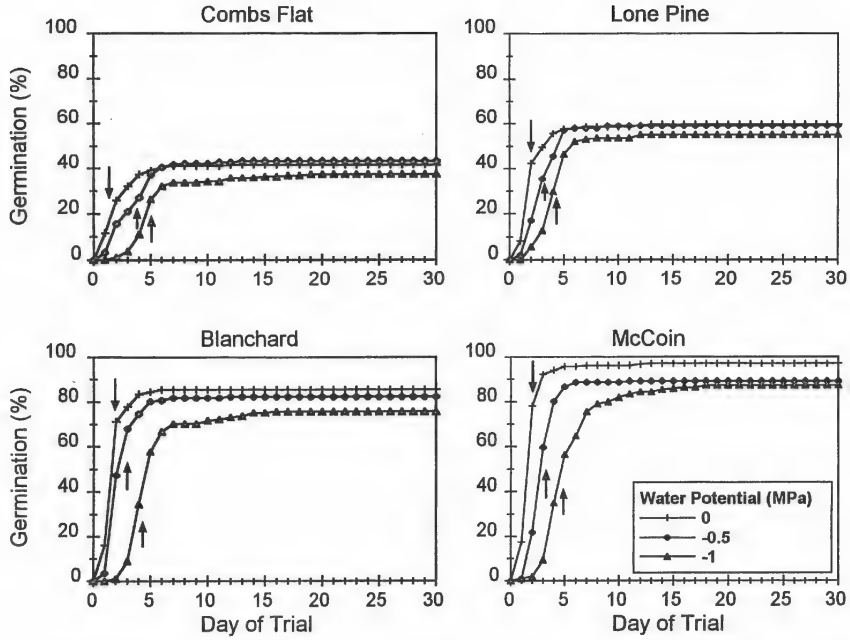

Figure 6. Cheatgrass seed germination under conditions simulating September in central Oregon for four populations. Arrows as in Fig. 2.

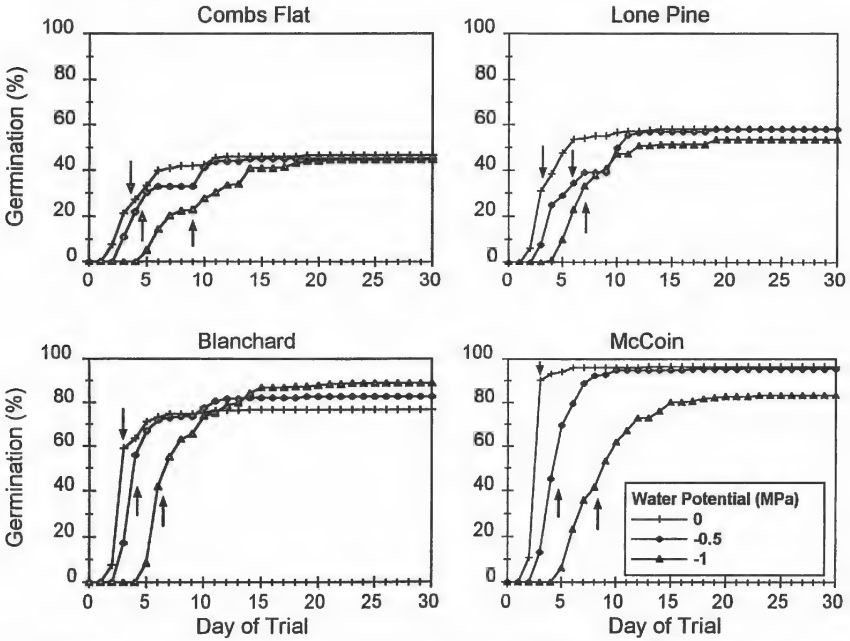

Figure 7. Cheatgrass seed germination under conditions simulating October in central Oregon for four populations. Arrows as in Fig. 2.

TABLE 3. Two-way interaction means for the coefficient of the rate of germination (CRG) of cheatgrass seeds in the August, September, and October experiments.

Ψ	Population			
(MPA)	Combs Flat	Lone Pine	Blanchard	McCoin
August				
0	8.63Aa	13.38Ba	22.64Ca	22.15Ca
-0.5	6.97Aa	6.94Ab	13.01Bb	13.07Bb
-1.0	2.30Ab	3.85Bc	5.08Cc	6.07Cc
September				
0	10.83Aa	14.61Aa	23.58Ba	30.44Ca
-0.5	7.42Ab	10.29Ab	17.41Bb	15.49Bb
-1.0	3.69Ac	6.88Bc	8.35Cc	9.52Dc
October				
0	6.35Aa	8.23Ba	12.05Ca	16.91Da
-0.5	4.62Ab	5.42Ab	9.1Bb	10.34Bb
-1.0	2.56Ac	3.70Bc	6.11Dc	4.99Cc

Within an experiment, different uppercase letters indicate significant differences within a row; different lowercase letters indicate significant differences within a column (Fisher's LSD, α=0.05). August SE=0.7953. September SE=1.0572. October SE=0.4014.

et al. 1994). Cheatgrass seed germination is relatively insensitive to moisture and temperature stress (Young and Evans 1982; Thill et al. 1979; Harris 1967; this study). We interpret this as a strategy for winning a competition for soil moisture in a xeric climate: start growth and resource exploitation as soon as possible. We hypothesized that persistence of Idaho fescue on cheatgrass-invaded Oregon rangelands was due, in part, to rapid germination under conditions typical of autumn. Such a germination response would increase the likelihood of Idaho fescue seedlings successfully competing with neighboring cheatgrass because competitive ability is a function of production and placement of resource-absorbing surfaces (Grime 1979) and early emergence results in greater space capture (Samuel and DePuit 1987; Weiner 1985; Ross and Harper 1972). However, Idaho fescue seeds were slower to germinate than cheatgrass seeds. Because Idaho fescue seeds took 3-4 times as long to begin germinating as cheatgrass seeds (for example, 4 days versus 1 day given no moisture stress and September conditions), Idaho fescue seedlings are very unlikely to out-compete cheatgrass seedlings. Unless growth rates are much higher in Idaho fescue than in cheatgrass, which is unlikely as Idaho fescue is a perennial and cheatgrass an annual, Idaho fescue seedlings would lag behind cheatgrass in production of resource-absorbing leaves and roots and hence in resource uptake. Persistence of Idaho fescue on cheatgrass-invaded sites is not due to rapid germination placing native seedlings in a better competitive position relative to cheatgrass seedlings.

Idaho fescue is not more tolerant of moisture stress during germination than cheatgrass. Percent germination of Idaho fescue seeds was reduced and days to germination and median response times increased with increasing water stress. Percent germination of cheatgrass seeds largely remained constant over the range of water potential tested. Increasing water stress slowed cheatgrass seed germination, but the effect was much less pronounced than in Idaho fescue. The response variable which integrates rate and extent of germination, CRG, was consistently greater, usually much so, for cheatgrass seeds than for seeds of Idaho fescue.

Because neither rapid germination and resultant competitive positioning nor reduced sensitivity to moisture stress during germination overcome the competitive advantage of cheatgrass, the question of recruitment into persisting Idaho fescue populations remains. Idaho fescue seedlings on cheatgrass-invaded sites are likely to experience severe moisture stress caused by earlier-emerging, faster-growing cheatgrass neighbors. Perhaps recruitment of Idaho fescue is limited to periods of exceptional moisture availability, when survival requirements can be met despite neighboring cheatgrass. After-ripening requirements of Idaho fescue seeds assure that 35% of the seed crop remains dormant for six months following dispersal (Goodwin et al. 1995), by which time winter precipitation has (usually) recharged soil moisture. Idaho fescue evolved in a xeric climate where periodic drought is common, that is, selection would promote tolerance of moisture stress. Idaho fescue seedlings may require less moisture than cheatgrass seedlings. Germination after soil moisture has been recharged, coupled with unusually frequent precipitation during spring may allow Idaho fescue seedlings to establish on cheatgrass-invaded sites. If such a seedling were able to survive summer drought, it would have at least a transient advantage over cheatgrass seedlings the following fall: cheatgrass would have to establish from seed while the Idaho fescue seedling would have an established root system. The improbability of such abundant soil moisture over

such an extended time makes it difficult to believe this mechanism could sustain a population. However, if vegetative propagation (fragmentation and formation of clones, see Samuel and Hart 1995) confers great longevity to Idaho fescue, and because mature individuals compete successfully with cheatgrass (Borman et al. 1991), such infrequent recruitment may allow population maintenance (Lauenroth et al. 1994) and provide the diversity of genotypes required for selection and evolution.

Cheatgrass seeds from the McCoin population averaged 90.5% germination in the three experiments, and Blanchard seed 82%. Germination was considerably poorer in Lone Pine and Combs Flat collections, with 57% and 44.5% germination, respectively. The poor germination of Lone Pine and Combs Flat cheatgrass seed was surprising. All seeds used in these experiments were collected, threshed, and cleaned in summer and fall of 1989. The seed lots were two years old, well within the longevity of stored cheatgrass seeds (Hulbert 1955), when germination tests were conducted. Many cheatgrass seeds which failed to germinate had lost their lemma and palea in processing. These two structures are important in enforcing dormancy in the grass embryo (Simpson 1990), and grass seeds lacking lemma and palea have reduced longevity in storage (Benech Arnold et al. 1992; Justice and Bass 1978). The disparity in seed viability remains an interesting question, however, as all cheatgrass seed lots were processed in the same manner. Additionally, there were no differences in seed mass among the four collections (Goodwin 1993), suggesting they had full compliments of endosperm. Of the four sites, Combs Flat and Lone Pine are in lower ecological condition than other sites. Blanchard seed was collected from a narrow, rocky fence row which provided a refuge from grazing livestock. The McCoin site is in the best condition. Grazing leads to nutrient redistribution and export from native rangelands, particularly of nitrogen (Woodmansee 1978; Archer and Smeins 1991). The greater susceptibility of the Lone Pine and Combs Flat seed to mechanical injury may be a maternal effect caused by nutrient deficiency. Soil analyses showed low nitrogen levels at these two sites, particularly of NO_3-N, but the Blanchard site is also nitrogen poor (Goodwin 1993). Unfortunately, we did not analyze seed tissues for nutrient concentrations. A genetic basis for susceptibility to injury cannot be ruled out, but is unlikely given extremely low genetic variation in cheatgrass (Novak et al. 1991). Such effects were not seen in Idaho fescue: the Combs Flat and Lone Pine populations of Idaho fescue seed were not consistently poor performers. This difference between the two species is probably due to their different life histories. A rapidly growing annual such as cheatgrass is more sensitive to a limited nutrient supply than is a slow-growing perennial (Grime 1979; McLendon and Redente 1992; Redente et al. 1992).

Moisture for imbibition is the most influential factor affecting germination of after-ripened (nondormant) seeds of Idaho fescue and cheatgrass. The two species illustrate strategies associated with different life histories. High temperatures inhibit Idaho fescue seed germination; high temperature and high moisture stress in shrub steppe have selected germination requirements that increase the probability of available soil moisture. Idaho fescue, a perennial, reduces risks of seedling mortality by waiting for wetter soils. Cheatgrass shows a strategy typical of ruderals (Evans and Etherington 1990): reduced sensitivity to environmental conditions and rapid germination at greater risk of seedling mortality. Desiccation is the major cause of death among autumn cohorts of cheatgrass seedlings (Mack and Pyke 1984). Seedling survival on Intermountain rangelands is greatly influenced by the temporal distribution of rainfall. Long-term climate records show August to be the warmest and driest month of the year in central Oregon. Seedlings emerging in August are very likely to die from lack of moisture. September is a wetter month, averaging about twice as much precipitation as August, and October is wetter still. November is even wetter than preceding months but mean daily temperature is so low (3.4 °C) that growth is inhibited. October temperatures are more favorable for growth (mean daily temperature = 9.2 °C), but seedlings emerging in October would soon be subject to inhibitory temperatures in November. Emergence in September would allow up to nine weeks of growth before low temperatures induced dormancy, and both Idaho fescue and cheatgrass had the highest CRGs under September conditions. Mack and Pyke (1983) suggested the existence of fairly well-defined periods during which autumn emergence is late enough to escape desiccation but early enough to allow sufficient growth to survive any subsequent grazing or winter injury.

Germination during September offers the best compromise between moisture availability and favorable temperatures to be had in late summer and autumn in central Oregon.

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Habitat Characteristics and Morphological Differences of *Trifolium thompsonii* Populations

Abstract

Trifolium thompsonii (Morton) is a rare and threatened legume of the Eastern Cascades previously known only in Swakane Canyon of Chelan County, Washington. Recent wildfire disturbances and new population sightings prompted investigation of the habitat characteristics of this taxon. Transect sampling and cluster analysis identified *T. thompsonii* occurrence in four plant associations: *Pseudotsuga menziesii/ Calmagrostis rubescens* (PSME/CARU), *Pinus ponderosa/ Agropyron spicatum* (PIPO/AGSP), *Artemisia tridentata/ Agropyron spicatum* (ARTR/AGSP), and *Artemisia tridentata-vaseyana/ Agropyron spicatum* (ARVA/AGSP). Thompson's clover occurs in a mosaic pattern characteristic of fire disturbed and grazed communities with 24-69 percent cover of forbs and grasses and 0-36 percent cover of trees and shrubs. Morphological expression of *T. thompsonii* ranged from tall (32 cm) multifloral stands in mesic PSME to relatively small (25 cm) individuals with only one flowerhead in the xeric ARTR. In contrast, plant density was low in PSME at 0.6 plants-m^{-2} but high in ARTR at 6.4 plants-m^{-2}. This study confirms *T. thompsonii* to be a vigorous and dominant forb component of early seral communities in the ponderosa pine-shrub steppe ecotone.

Introduction

Trifolium thompsonii (Morton) is one of 12 plant species listed as threatened along the eastern slope of the Washington Cascades. The taxon is among several under study in the Wenatchee area where about 15 percent of the threatened, endangered and sensitive species of Washington state occur (Washington Natural Heritage Program 1994). J.W. Thompson first reported its occurrence in 1933 on the slopes of Swakane canyon at the edge of *Pinus ponderosa* forests and into the *Artemisia tridentata* shrub steppe adjacent to the western shore of the Columbia River (Hitchcock et al. 1969). Work by Canfield (1977) and Tiedemann et al. (1977) expanded knowledge of this species and documented 10 additional stands, the largest located within the 80 ha Thompson's Clover Research Natural Area. Survey work reported by Gamon and Sprague (1988) further recorded the Chelan county occurrences of *T. thompsonii* in canyons near the Entiat River. They also reported on a stand east of the Columbia River, about 6 km southeast of the Thompson's Clover Research Natural Area.

These new sightings suggest a wider range potential and perhaps a different ecological amplitude than previously described (Kennison and Taylor 1979). The purpose of this study was to clarify the habitat characteristics of *T. thompsonii* and describe plant responses of this species to habitat changes among its associated plant communities. The objectives of this research were: 1. To document the vegetative communities and site factors associated with *T. thompsonii*; and 2. Compare morphological features and plant density of *T. thompsonii* populations among these vegetative communities.

Methods

Study Area

The known range of *T. thompsonii* is the area north of the Wenatchee River (47°23'43"N, 120°19'23"W) to the Entiat River (47°39'51"N, 120°13'23"W) and within 4 km of each side of the Columbia River. The nearest climate station at Wenatchee, Washington (elevation 343 m), has a mean January temperature of -3°C and a mean July temperature of 22°C. Annual precipitation is about 220 mm occurring mostly as snow between November and April. This taxon was reported to occur at elevations ranging 345 m to 1146 m (Canfield 1977, and this study). Using the normal lapse rate of 2°C per 300 m, the mean temperature on the study sites would be -8°C for January and 17°C for July. At these elevations, winter snowpack could remain for up to 60 days longer than in the valley floor and would delay bud emergence for *T. thompsonii* and other species (Gamon and Sprague 1988).

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Disturbance History

Fire has been an historical disturbance agent in this region (Agee 1993) and was evident by fire-scarred tree stems and bunchgrass culms on the Chelan county portion of the study area. Figure 1 shows the pattern of wildfire within the known range of *T. thompsonii* (Canfield 1977, WNF 1990). The most recent fire event among *T. thompsonii* populations was the 17,000 ha Dinkleman burn of July 1988. Sheep and cattle grazing occurred in this area from the late 1800s until 1965 (Dow 1964, Tiedemann et al. 1977). No known fires have recently occurred on the Douglas County study sites. However, the area is presently grazed seasonally by domestic cattle and some of the land is cultivated for wheat (E. Gutzwiler 1993, personal communication).

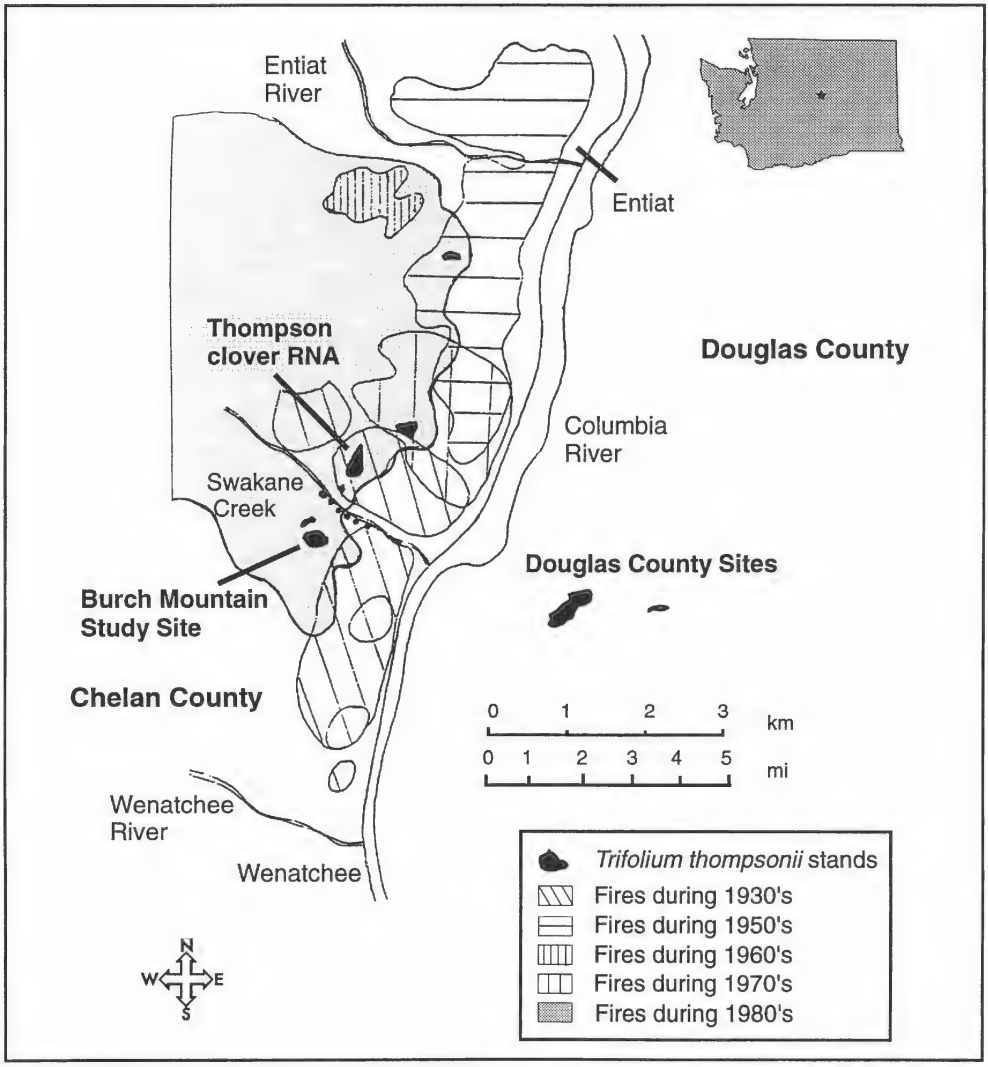

Figure 1. Present known stands of *T. thompsonii* in Chelan and Douglas Counties, Washington and known areas of fire disturbance in *T. thompsonii* range since 1930 (adapted from Canfield 1977 and WNF 1990).

Field Sampling

Study sites were selected from maps of known *T. thompsonii* locations (Gamon and Sprague 1988). We sampled in five of the eight known locations including a newly discovered site in Douglas County. Populations at two of the remaining stands (Tenas George and Keystone Point) were not located and we could not access the last location (Keystone canyon) due to road closure. The criterion for sample site selection was the presence of a stand of this taxon greater than 50 m diameter. The locations sampled were one site at Thompson's Clover Research Natural Area, two sites on Burch Mountain, and two sites on private property in Douglas County (see Figure 1). These five areas were distinct in physical characteristics and disjunct such that selection of one area was independent of another.

Vegetation was systematically sampled in each study area by placing a 50 cm x 20 cm wire frame in a 4 by 5, 20 frame block at three positions (0, 30, 50 m) along a randomly placed 50 m tape transect running through *T. thompsonii* patches (Brower et al. 1990 and see Figure 2). The three blocks together constituted sampling of a patch of *T. thompsonii* for a total of 20 patches among the five locations studied. The vertically projected canopy cover (Daubenmire 1959) of each species encountered in the plot frame was recorded. Plant species identification followed Hitchcock and Cronquist (1973) and a list of plant names of Washington (USDA-SCS 1983). Soil surface condition was sampled at 10 painted points equally spaced on the plot frame as either litter, bare soil, plant presence, cryptogamic crust, wood pieces, or rocks. The density of *T. thompsonii* was recorded by counting individuals within 10 one-m^2 plot frames that were arranged in a block of two rows of five which overlayed the block of 20 vegetative sample plot frames (Figure 2). From each sample block at least 10 *T. thompsonii* individuals were selected and measured for morphological features that included height, leaf number, shoot number, flowerhead number and root crown diameter.

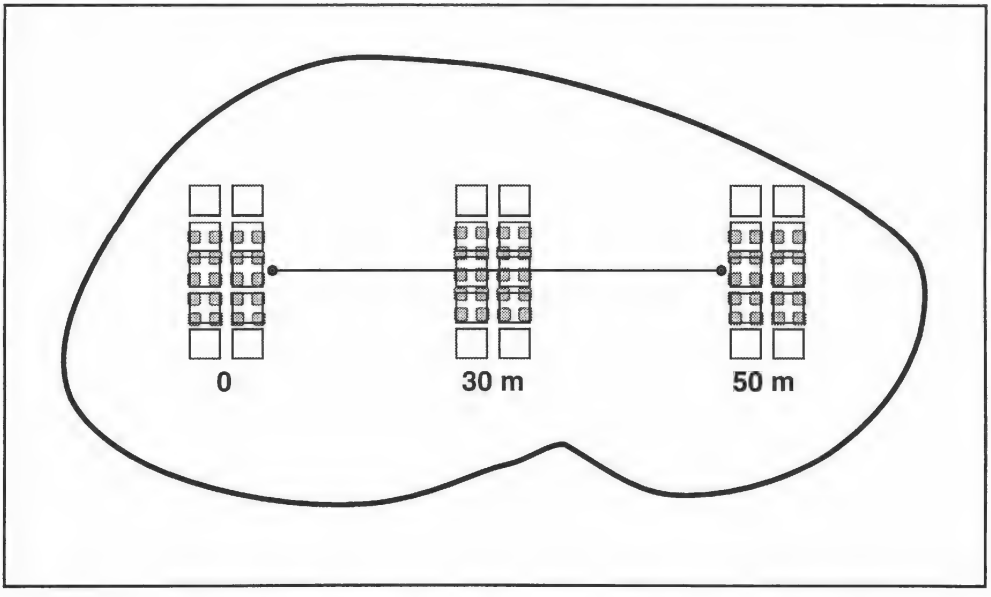

Figure 2. Pattern of sampling in a stylized sample patch of *T. thompsonii*. Canopy cover of each species was obtained by sampling in shaded blocks which are 20 plot frames, each 20 cm X 50 cm, spaced 50 cm each direction. The three block sub samples were aligned on a 50 m transect within the sample patch. Density of *T. thompsonii* was obtained by placing 10-1 meter X 1 meter plot frames in two rows of five overlaying the approximate area covered by the plot frame matrix and counting individuals.

At each sample block site the following site characters were recorded: elevation, slope, aspect, slope position, and microterrain feature (e.g., flat, convex, concave). Additional information on study area soils was from Soil Conservation Service soil survey (Beiler 1969, 1978).

Analysis

The means of species canopy cover from each block were used in a Systat Statistics cluster analysis procedure to identify major plant communities associated with *T. thompsonii* (Wilkinson and Hill 1992). We calculated mean canopy cover and frequency values for all species in each sample patch. We graphed density of *T. thompsonii* and measurements of the species' morphological features for comparison by plant community (Figure 3). The morphological features were logarithmically transformed to normalize data and subjected to analysis of variance to test for differences among community types. A regression analysis was used to examine the relationship between *T. thompsonii* density and tree density.

Results and Discussion

Trifolium thompsonii occurred in three broad vegetative settings: forest patches, steppe-like parklands, and semiarid shrub steppe. The forest patches occurring on mesic topographic settings such as gullies and northerly slopes, consisted of a layered community of trees, shrubs, grasses, and forbs dominated by *Pseudotsuga menziesii*. Steppe-like parklands were grass dominated landscapes with occasional *Pinus ponderosa* individuals. The shrub steppe consisted of the drought-tolerant, tall shrub-bunchgrass (*Artemisia tridentata/Agropyron spicatum*) vegetative associations typical of the central Columbia Basin.

Within these three settings, four plant communities were identified using cluster analysis of

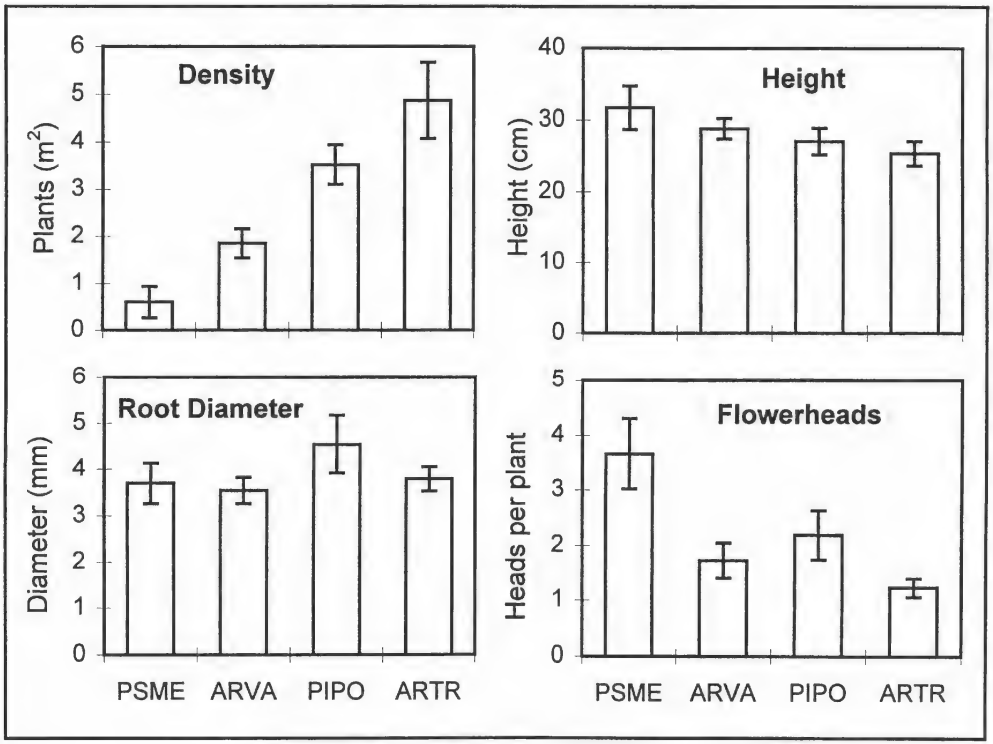

Figure 3. *T. thompsonii* population and morphological features in four community types. Vertical bars are 90% confidence intervals.

species composition and cover values from the sampling matrices. These four community types represented various successional stages of four plant associations described by Franklin and Dyrness (1973) and Daubenmire (1970). They are *Pseudotsuga menziesii/ Calmagrostis rubescens* (PSME/CARU) of the forest setting; *Pinus ponderosa/ Agropyron spicatum* (PIPO/AGSP), and *Artemisia vaseyana/ Agropyron spicatum* (ARVA/AGSP) of a steppe-like setting; and *Artemisia tridentata/ Agropyron spicatum* (ARTR/AGSP) of the shrub steppe setting. These four community types are described below with reference to vegetative composition and site factor data in Tables 1 and 2 and Figure 3.

Plant Community Descriptions

The PSME/CARU community occurred on north facing steep slopes (40-50 percent) at mid to upper elevations (> 1060 m) in Chelan County. This was in the wettest and coolest settings of this study with mean annual precipitation ranging from 508 to 1016 mm and mean annual temperature of 5-6°C (Bieler 1969). *Pseudotsuga menziesii* was the overstory dominant with *Pinus ponderosa* a codominant in some sample units. *Spiraea betulifolia* and *Penstemon fruticosus* were prominent shrub layer components. The grass, *Calmagrostis rubescens,* was a significant herbaceous dominant of this community type suggesting moist upper elevation site conditions. *Balsamorhiza sagittata, Achillia millefolium* and *T. thompsonii* were the most prominent forb species. Other important herbaceous species were *Festuca idahoensis, Bromus tectorum, Poa secundi, Colinsia parviflora, Crypthantha affinis,* and *Epilobium paniculatum.* In this community, located on Burch Mountain, the 1988 Dinkleman fire destroyed the crown foliage of nearly all *Pseudotsuga menziesii* and *Pinus ponderosa.*

Soil surfaces in PSME/CARU were litter covered due to the high proportion of shrub and grass cover (Table 2 and Figure 4). The soil profile was rocky and among the shallowest of those in this study, ranging from 35 to 48 cm in depth.

The ARVA/AGSP community was located on the Thompson's Clover Research Natural Area (Figure 1). Individuals of *Artemisia vasayana,* a montane ecotype of *A. tridentata,* and *A. tripartita* represented the overstory cover of this community type. The current vegetative dominants were the grass species *Agropyron spicatum, Poa secunda, Festuca idahoensis,* ranging in mean cover from 4 to 27 percent. *T. thompsonii, Balsamorhiza sagittata, Antennaria rosea,* and *Achillia millefolium* were the major forbs. Annuals were not prominent in this community, except for a *Bromus tectorum* coverage of 4 percent, the result of ground disturbance. Charred bunchgrass clumps and shrub skeletons indicated recent (1988) fire disturbance.

The elevation of this community ranged from 816-1071 m on 30-40 percent slopes facing north to southwest. Ground cover was mostly litter ranging from 37-69 percent and plant basal cover from 17-27 percent (Table 2). Estimated precipitation, soil depth and soil water availability were similar to PIPO/AGSP (Bieler 1969).

The dominant vegetation in PIPO/AGSP was an *Agropyron spicatum-Festuca idahoensis* grass understory (Table 1). *Pinus ponderosa* was present as solitary mature individuals across the Research Natural Area with canopy cover rarely exceeding 2 percent. Cover and density were higher in more mesic topographic settings of gullies and north slopes. The low shrubs, *Eriogonum heracleoides, Phlox longifolia, Haplopappus stenophyllus,* were present with less than 5 percent overall cover. No tall shrubs were recorded. The most prominent species in the forb component were *Antennaria rosea, Balsamorhiza sagittata, T. thompsonii* and *Achillea millefolium.* The annuals *Collinsia parviflora, Epilobium paniculatum,* and *Crypthantha affinis* were ubiquitous in the sample plots but had small cover values. Evidence of fire disturbance was generally in the grass shrub understory. There was no fire damage in tree crowns. The fire disturbances also explain the lack of fire-intolerant *Artemisia* spp. and *Purshia* spp. in the shrub component.

This community was sampled at elevations of 810-899 m on steep slopes with varied north to southwesterly exposures. Soil depths ranged 25-55 cm with estimated clay content of 1-4 percent (Bieler 1969).

Dominants in the ARTR/AGSP community type overstory were the tall shrubs *Artemisia tridentata* and *Purshia tridentata,* with mean canopy coverage values of 9 percent and 5 percent. The herbaceous dominants were *Agropyron spicatum, Festuca idahoensis,* and *Poa secunda* with up to 44 percent mean canopy cover. This community

TABLE 1. Constancy and mean cover values of species in four community types associated with *Trifolium thompsonii.*

	PSME		ARVA		PIPO		ARTR	
	N=2		N=3		N=7		N=9	
	Con	Cov	Con	Cov	Con	Cov	Con	Cov
Tree								
Pinus ponderosa	100	29.0	0	0.0	P	P	0	0.0
Pseudotsuga menziesii	100	32.0	0	0.0	0	0	0	0.0
Shrub								
Artemisia tridentata	0	0.0	0	0.0	14	Tr	77	8.5
Artemisia vaseyana	0	0.0	67	1.2	0	0.0	0	0.0
Artemisia tripartita	0	0.0	67	14.0	0	0.0	11	1.0
Ceanothus velutinus	50	6.0	0	0.0	0	0.0	0	0.0
Chrysothamnus viscidiflorus	0	0.0	0	0.0	0	0.0	11	0.2
Erigeron linearis	0	0.0	0	0.0	14	0.7	0	0.0
Eriogonum heracleoides	0	0.0	100	8.5	43	2.2	55	2.6
Eriogonum niveum	0	0.0	0	0.0	14	0.4	0	0.0
Eriogonum strictum	0	0.0	0	0.0	0	0.0	22	0.2
Haplopappus stenophyllus	0	0.0	0	0.0	14	Tr	55	1.2
Penstemon fruticosus	100	11.5	0	0.0	28	0.5	0	0.0
Phlox longifolia	100	1.8	34	0.8	57	1.7	100	3.3
Purshia tridentata	0	0.0	0	0.0	0	0.0	66	4.9
Ribes cereum	50	0.4	0	0.0	0	0.0	22	0.6
Spiraea betulifolia	100	12.7	0	0.0	0	0.0	0	0.0
Symphoricarpos albus	50	1.6	0	0.0	14	0.4	0	0.0
Vaccinium occidentale	50	2.3	0	0.0	0	0.0	0	0.0
Grass								
Agropyron cristatum	0	0.0	0	0.0	0	0.0	11	Tr
Agropyron spicatum	50	0.1	100	26.7	100	26.4	100	44.1
Bromus tectorum	100	0.4	67	4.4	57	2.0	88	1.4
Calmagrostis rubescens	100	37.0	0	0.0	0	0.0	0	0.0
Festuca idahoensis	100	3.7	34	4.2	100	7.5	88	14.5
Festuca rubrua	0	0.0	0	0.0	28	Tr	0	0.0
Koeleria cristata	50	0.1	100	4.3	71	2.3	0	0.0
Melica bulbosa	50	0.0	34	Tr	14	Tr	33	1.3
Poa secunda	100	1.2	100	5.0	85	4.1	100	7.1
Forb								
Achillea millefolium	100	7.1	100	2.4	100	7.3	77	2.0
Agoseris grandiflora	0	0.0	100	1.8	57	1.5	88	6.0
Allium acuminatum	0	0.0	0	0.0	0	0.0	77	10.7
Angelica arguta	0	0.0	0	0.0	14	Tr	0	0.0
Antennaria rosea	0	0.0	34	2.5	85	17.6	0	0.0
Astragalus purshii	0	0.0	0	0.0	43	1.3	0	0.0
Balsamorhiza sagittata	100	9.9	67	3.8	100	11.7	100	17.6
Brodiaea douglasii	0	0.0	34	0.3	0	0.0	11	Tr
Castelleja lutescens	50	0.1	0	0.0	28	0.5	22	0.1
Collinsia parviflora	100	0.5	100	0.9	100	3.1	66	1.0
Cryptantha affinis	100	0.9	67	0.8	85	1.5	22	0.1
Epilobium paniculatum	100	1.6	100	1.2	100	3.2	44	TR
Geum triflorum	50	1.6	34	0.9	28	1.3	0	0.0
Helianthus petiolaris	0	0.0	0	0.0	28	2.4	0	0.0
Heuchera cylindrica	0	0.0	0	0.0	28	Tr	0	0.0
Hieracium albiflorum	50	0.8	34	0.9	57	1.5	11	Tr
Lactuca serriola	0	0.0	0	0.0	14	0.4	11	0.3
Linanthus liniflorus	0	0.0	0	0.0	14	Tr	0	0.0
Lithospermum ruderale	0	0.0	0	0.0	0	0.0	11	Tr
Lomatium nudicule	50	0.4	0	0.0	57	1.6	77	3.5

TABLE 1. (Continued)

	PSME		ARVA		PIPO		ARTR	
	N=2		N=3		N=7		N=9	
	Con	Cov	Con	Cov	Con	Cov	Con	Cov
Lupinus leucophyllus	0	0.0	0	0.0	0	0.0	44	1.3
Lupinus sericeus	0	0.0	34	Tr	71	1.4	66	2.8
Madia glomerata	0	0.0	0	0.0	14	Tr	0	0.0
Microsteris gracilis	100	0.4	100	1.0	57	0.2	77	1.6
Polemonium micranthum	0	0.0	34	0.2	57	0.2	100	0.6
Sisymbrium altissimum	50	0.4	67	1.2	0	0.0	22	0.1
Trifolium thompsonii	100	6.5	100	11.6	100	20.7	100	21.2

Notes: P= P. pine occurs in clusters and individuals. Aerial photo verifications indicate cover range 2- 12% on 80 ha. Tr= cover value less than 0.1 in sample plot. Community type abbreviations are: PSME= *Pseudotsuga menziesii/ Calmagrostis rubescens*; PIPO= *Ponderosa pine/ Agropyron spicatum*; ARTR= *Artemisia tridentata/ Agropyron spicatum*; ARVA= *Artemisia tridentata-vasayana/ Agropyron spicatum*

TABLE 2. Range of values for site factors in four community types associated with *Trifolium thompsonii*

	PSME	ARVA	PIPO	ARTR
Site Variables				
Elevation (m)	1115-1060	816-1071	810-899	890-1096
Slope (%)	40-50	30-40	30-60	15-50
Aspect (deg)	360	360-235	360-235	045-270
Precipit (mm)	508-1016	304-406	304-406	208-620
Temp (C)	5-6	8-10	8-10	8-10
Soil Surface				
Litter (%)	44-63	37-69	40-60	19-69
Bare Ground (%)	11	8-40	8-34	13-58
Rock (%)	1	0	0	0-26
Wood (%)	4-11	0	1	0-10
Basal Area (%)	18	17-27	11-29	17-27
Cryptogams (%)	1-4	0-1.5	1-4	5
Soil Profile				
Depth (cm)	35-48	48-56	25-55	24-75
Bulk Density (g/cc)	1.22-1.40	1.21-1.29	1.10-1.30	1.05-1.30
Available Water (cm-cm)	0.38-0.43	0.30-0.35	0.43-0.50	0.15-0.53
pH	6.5	6.4	6.4	7.1
Organic Matter (%)	2.5-4.5	2.6-3.0	2.8- 6.4	1.5-4.5
CEC (meq)	10-20	8.4-12.0	9-15	8-18
Coarse Fragments (%)	10-40	10-20	10-20	5-45
Sand (%)	72-83	67-68	65-79	33-59
Silt (%)	15-21	25-32	19-31	36-53
Clay (%)	1-3	1-6	1-4	2-13

Notes: Community type abbreviations are: PSME = *Pseudotsuga menziesii/ Calmagrostis rubescens*; PIPO = *Ponderosa pine/ Agropyron spicatum*; ARTR = *Artemisia tridentata/ Agropyron spicatum*; ARVA = *Artemisia tridentata-vasayana/ Agropyron spicatum*

was rich in forbs with 17 recorded. The most ubiquitous were *T. thompsonii*, *Balsamorhiza sagittata*, *Allium acuminatum*, *Agoseris grandiflora*, *Lomatium nudicule*, *Achellia millefolium*, and *Lupinus sericeus*. There was no field evidence or recorded documentation of recent fire in this community. However, some forbs and bunchgrasses appeared lightly grazed.

This community type occurred at elevations ranging 890 to 1096 m on 15-50 percent slopes

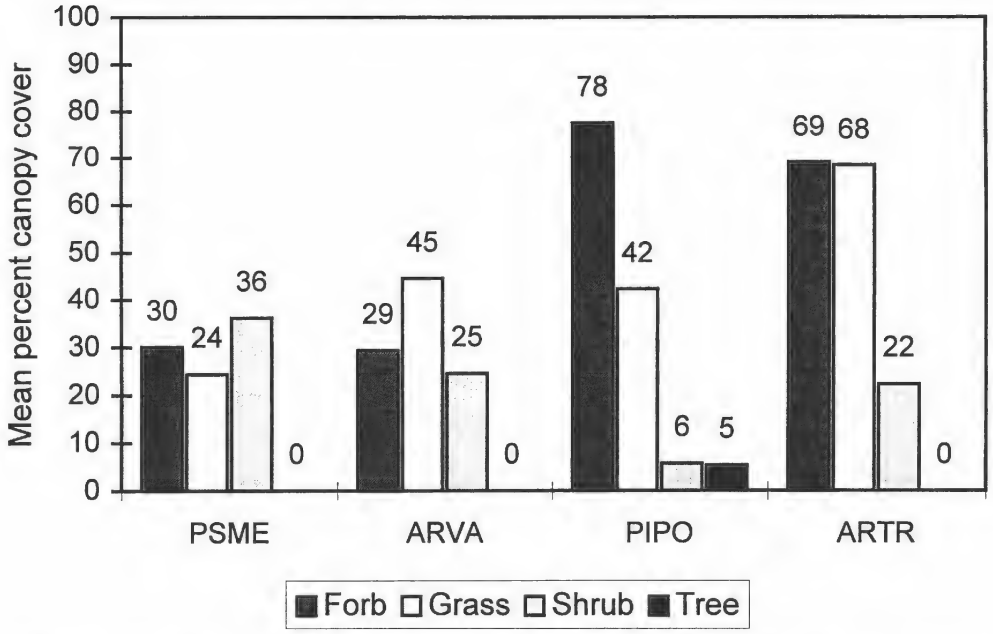

Figure 4. Canopy coverage by lifeform for four community types associated with *T. thompsonii*. No live trees on PSME due to fire kill.

with north to southwest exposures. It was the most xeric of the communities reported here. Modest clay content and varying soil depths accounted for the wide range in soil water availability values (Table 2). Soil surfaces here varied as indicated by higher proportions of bare rock surface cover.

Community Structure

Figure 4 shows vegetative structure of the four communities by layers of vegetative component. Grasses and forbs were prominent in the communities of PIPO, ARTR, and ARVA with forbs nearly equal in presence but more variable in cover and species composition among the groups. Note a relatively low value of shrub cover but high value of forb cover in PIPO/ AGSP; a probable result of recent fire disturbances since many tree boles displayed charred bark. Structure data also showed less cover of shrubs and trees and greater cover of grass and forb components from more mesic forest settings to the arid shrub steppe. This is likely the result of less precipitation at lower elevations (Table 2).

Plant Density—*T. thompsonii*

Density of *T. thompsonii* ranged from 0 to 16 plants-m^{-2} on 256 plots from within the four community types. Plant densities were significantly greater in ARVA, PIPO and ARTR than in PSME setting at 0.6 plants m^2 (Table 3). Specifically, plant density was highest in parts of the ARTR shrub-steppe of Douglas county where 1-m^2 plot frame samples contained as many as 16 plants. The ARTR

TABLE 3. Mean density (plants-m^2) of *T. thompsonii* in four community types

	PSME	PIPO	ARTR	ARVA
Density (m^2)	0.6	3.5	4.8	1.8
Standard error	0.19	0.25	0.47	0.18
p =	0.000	0.000	0.010	0.000
N =	20	99	88	49

Note: p = significance probability (<.05 is significant). N = number of plot frame samples. Community type abbreviations are: PSME = *Pseudotsuga menziesii/ Calmagrostis rubescens*; PIPO = *Ponderosa pine/ Agropyron spicatum*; ARTR = *Artemisia tridentata/ Agropyron spicatum*; ARVA = *Artemisia tridentata-vasayana/ Agropyron spicatum*

community had high grass coverages, particularly *Festuca idahoensis* with 56 percent cover (Table 1). It also had the deepest soils and highest silt content among the communities (Table 2). In contrast, plots sampled in the forested PSME were high in tree coverage and had shallow soil depths. Forest vegetation types and forest soil conditions may contribute to the low density value of 0.6 plants per square meter. Tree counts vs. *T. thompsonii* counts showed a slight negative correlation but a regression analysis of the data did not prove to be significant. We were unable to demonstrate that *T. thompsonii* stands are more suited to the heliophytic conditions of the open parks and shrub steppe within its range.

Morphological Characteristics—*T. thompsonii*

Considering mean values, a "typical" *T. thompsonii* specimen might be 27.6 cm in height, a three stem plant with five leaflets per leaf, two flowerheads and root diameter of 4 mm. A mean plant height of 31.7 cm for *T. thompsonii* in PSME was significantly ($p=0.010$) taller than in ARTR at 25.3 cm. There were no significant differences in height among ARVA, PIPO and ARTR. The number of flowerheads per plant in PSME was 3.6. This was significantly ($p=0.000$) greater than in the other community types, among which were no significant differences in flowerhead counts. Leaf and shoot counts did not significantly differ among the community types. Root crown diameters of 4.54 mm in PIPO were nominally greater than in the other community types but only significantly greater ($p=0.064$) than in the ARVA community at 3.54 mm.

The taller plants with more flowerheads in the PSME community suggests a slightly more robust *T. thompsonii* stand here. This may be a short-lived response to resource release since the PSME locations were burned by wildfires in 1988 and sampled in 1991. We hypothesize that *T. thompsonii* stands occurring in the PIPO community might be viewed as "typical." Plant heights of 27 cm, two flowerheads per plant, three stemmed plants and a larger root diameter suggests a greater period of site occupancy. However, it may be that the site is more frequently disturbed by wildfires and that *T. thompsonii* roots may be benefiting from the resource releases facilitated by the fires. There is an observable contrast in the smaller plants of the ARTR community of Douglas County vs. those in Chelan County, particularly the robust *T. thompsonii* of PSME on the Burch Mountain location, even though this study has not statistically substantiated this observation in all features. We suggest that precipitation availability and frequency of disturbances are likely to affect morphological differences of expression for this species among these documented habitats.

Recently Discovered Populations

In 1983 and 1993, two new populations of *T. thompsonii* were encountered in Douglas County. They were about 8 km east of the best known stands of Swakane canyon (Gamon and Sprague 1988 and this study). The landscape and terrain features of the Douglas County study area are similar to those west of the Columbia River. It features steep hillslopes rising to forested summits at 1300 m with a sharp ecotone into grass-shrub ecosystems at about 1150 m elevation. A distinct difference in the vegetative composition is the ubiquitous and relatively even coverage of *Artemisia tridentata* and *Purshia tridentata* on this landscape, indicating infrequent stand-altering fire events. The primary disturbance feature here is the agricultural activity of wheat fields and associated cattle grazing.

Trifolium thompsonii occurs here in disjunct patches ranging from 2 m^2 to about 10 ha in size, often in close proximity to *A. tridentata* individuals. Native bunch grasses are prominent vegetative cover and *T. thompsonii* is often the dominant forb. *Trifolium. thompsonii* in the Douglas county samples was typically a shorter individual with only one or two flowerheads (Figure 3). Population densities were significantly larger than those found west of the Columbia River (Figure 3). Total canopy coverage of vegetation in Douglas County plots was greater than the other sites sampled in this study (discounting the tree category in PSME, since the crown foliage was removed by fire). *Trifolium thompsonii* stands were 2-3 km from the nearest forest ecotone in the midst of well-developed *A. tridentata/ Agropyron spicatum-F. idahoensis* associations.

The *T. thompsonii* population expression in Douglas County was different from that of the Chelan County populations. The reasons for the differences are speculative. *Trifolium thompsonii* stands east of the Wenatchee river are functioning in relatively undisturbed habitat. The smaller stature of the plant may be due to the more xeric climate and soil conditions (Table 2). The smaller plant

heights could also be an effect of the greater vegetation cover of this site: a greater community biomass competing for a limited pool of resources.

Conclusions

There is increased interest by land managers in the biology and habitat conditions of rare species particularly on Wenatchee area landscapes which have been historically (and recently in 1994) frequented by large scale fires. This study clarifies that *T. thompsonii* habitat is best characterized by the plant association featuring *Artemisia tridentata / Agropyron spicatum-F. idahoensis*, as demonstrated in the mature community of the Douglas county sample sites. This habitat type association forms an integrated ecotone along the forested edge near the summits of the arid foothills near Wenatchee. *Trifolium thompsonii* is likely an ancient endemic of the *Artemisia tridentata* habitat type, however, *A. Tridentata* is often absent due to wildfire events. *Trifolium thompsonii* seems to respond to fire-caused openings in adjacent forested settings with vigorous growth and flower production, probably a physiological response to resource release. As tree or shrub canopy cover increases, *Trifolium thompsonii* vigor is reduced as indicated by the Douglas County samples. Since there are no clear explanations for the limited range of this species, new population locations are probable. New stands will likely be found in both disturbed and undisturbed *A. tridentata* habitat types and in disturbed forested settings near the shrub-grass ecotone.

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Forest Fertilization with Biosolids: Impact on Small Mammal Population Dynamics

Abstract

This study was designed to measure the effects of a biosolids (sewage sludge) fertilization application on resident small mammal populations in young coastal coniferous forest near Maple Ridge, British Columbia, Canada. Populations of the deer mouse (*Peromyscus maniculatus*), Oregon vole (*Microtus oregoni*), Townsend chipmunk (*Eutamias townsendii*), shrews (*Sorex* spp.), and a few species caught occasionally, were sampled in replicated control and treatment study sites from May 1990 to October 1991. Sludge application occurred in November 1990. There were no detectable differences in the abundance of deer mice, Oregon voles, and chipmunks on treatment areas relative to controls after sludge application. This was also the case for recruitment, survival, mean body weight and species diversity. There was, however, a significant increase in the growth rate of juvenile deer mice on post-treatment sites. We conclude that there was no apparent effect on population parameters attributable to sludge treatment one year after application. Silvicultural applications of biosolids likely have less impact on small mammal populations than other forestry practices such as harvesting and slashburning.

Introduction

The future disposal of sewage sludge (biosolids) has become a problem of major concern. With the recent increase in environmental awareness, disposal of sludge in landfills is not only becoming unacceptable to the public, but it is also prohibitively expensive in terms of transportation costs. This problem is expected to escalate because suitable disposal sites are becoming scarce and distant from city centers. As discussed by Kimmins et al. (1992), there are six options to sewage disposal: (1) agricultural land application, (2) top soil production and composting, (3) landfill cover and gravel pit reclamation, (4) silvicultural application, (5) mine reclamation, and (6) rangeland improvement.

Five constituents in sludge are considered in determining suitable end usages of sludge. These are organic content, nutrients, pathogens, trace metals and toxic organic chemicals/synthetic organics. The organic content in sludge contains numerous essential nutrients necessary for plant growth, the most notable ones being nitrogen, phosphorus and potassium. Unfortunately, sludge also contains pathogens, a significant number of which can become concentrated in sludge during the wastewater treatment process. Thermophilic digestion or irradiation can destroy a large proportion of these pathogens. However, since most sludges do not contain enough of these pathogens to warrant great concern, this process is often not done due to its high cost. Trace metals and inorganic ions such as arsenic, boron, cadmium, copper, lead, nickel, mercury, silver, and zinc are also constituents of sludge. In small concentrations, these can serve as essential micronutrients. In high concentrations, they may be toxic to humans, plants, and animals (Zasoski 1981, West et al. 1981).

Major concerns associated with use of biosolids for forest fertilization include potential adverse effects on wildlife, heavy metal contamination in both surface or ground waters, and introduction of parasites or pathogens into the ecosystem (Raedeke and West 1986). Research from Washington State's Pack Forest in recent years has demonstrated significant responses in tree growth on some sites. In general, no 'unacceptable' environmental consequences were found (Cole et al. 1986, Henry 1989), although the majority of past studies on the effects of sludge on wildlife considered only animal abundance and heavy metal accumulation.

West et al. (1981) found that of the small mammal species they studied, abundance of insectivores (shrews) and gramnivores did not differ between control and sludge-treated sites, but abundance of herbivorous small mammals was significantly lower on treatment than control sites. Taber and Zasoski (1980) found increased accumulations of cadmium and lead in the kidneys and livers of two species of insectivores and an

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omnivore/gramnivore mammal. Although metal levels were too low to be considered physiologically harmful, this may become a consideration when sludge treatments are re-applied periodically over an extended period of time. Examination of a shrew population found no conclusive evidence of population decline despite increased metal accumulations (Hegstrom 1986). No studies have evaluated the impact of these biosolids on population dynamics of small mammals in young forests.

Our study was designed to test the hypothesis that a sewage sludge application for forest fertilization would adversely affect abundance and related population parameters of several species in a small mammal community.

Materials and Methods

Description of study areas

This study was located at the University of British Columbia Malcolm Knapp Research Forest near Maple Ridge, B.C., Canada. The treatment study area (13 ha) was clear-cut harvested in 1973, slashburned in the fall of 1974 and planted with Douglas-fir (*Pseudotsuga menziesii*) in the spring of 1975. The area was previously covered with a mature (70- to 90-year-old) forest dominated by western hemlock (*Tsuga heterophylla*), Douglas-fir and western red cedar (*Thuja plicata*) (Feller 1977). Cover included well decomposed slash with an abundance of deciduous trees, shrubs and herbaceous vegetation. Associated with the Douglas-fir stand were western hemlock natural regeneration and red alder (*Alnus rubra*), paper birch (*Betula papyrifera*), willow (*Salix* spp.), vine maple (*Acer circinatum*), black raspberry (*Rubus leucodermis*) and salmonberry (*Rubus spectabilis*). Bracken fern (*Pteridium aquilinum*) and fireweed (*Epilobium angustifolium*) were the dominant herbaceous annual species. Two 1-ha sites within this area were treated with sewage sludge. Treatment-1 was located on a dry upper slope, treatment-2 at a lower, mid-slope site and spaced approximately 250 m from treatment-1.

The control study area (15 ha) was clear-cut in 1973 and planted with Douglas-fir in 1975. This area was not burned. The previous forest was also dominated by mature western hemlock, mixed with Douglas-fir and western red cedar. The main cover was well decomposed slash with a similar vegetation composition as the treatment study area. Two sites (control-1 and control-2) 250 m apart were situated at similar elevations as those in the treatment. Thus, these four experimental sites were considered as paired control-treatment units. Control and treatment study areas were separated by approximately 1200 m which was a sufficient distance to limit small mammal dispersal between the two areas.

All sites were considered mesic and located in the Coastal Western Hemlock biogeoclimatic zone (CWH_{dm}) (Meidinger and Pojar 1991) between 140 and 400 m in elevation.

Livetrapping Protocol

From May 1990 to October 1991, two treatment and two control grids were livetrapped at 3-week (spring, summer, and fall) and 6- to 8-week (winter) intervals with Longworth live traps. On each grid, 49 (7 x 7) trap stations were located at 14.3-m intervals with one live trap placed within a 2-m radius of each station. Traps were baited with oats and a slice of carrot for moisture, and coarse brown cotton for bedding. Traps were set on day 1, checked on days 2 and 3, and then locked open between trapping periods.

All small mammals captured, except shrews (*Sorex* spp.) and weasels (*Mustela* spp.), were ear-tagged with fingerling fish tags, sex was determined, reproductive condition noted, and weighed on Pesola spring balances. The duration of the breeding season was noted by palpation of male testes and the condition of mammaries of the females (Krebs et al. 1969). Small mammals were released immediately after processing. Shrews which died in the traps due to the overnight-trapping technique were recorded as to their station of capture, collected and frozen for later species identification.

Small mammal species encountered included the deer mouse (*Peromyscus maniculatus*), Oregon vole (*Microtus oregoni*), red-backed vole (*Clethrionomys gapperi*), Townsend chipmunk (*Eutamias townsendii*), Pacific jumping mouse (*Zapus trinotatus*), American shrew-mole (*Neurotrichus gibbsii*), two species of shrews (*S. vagrans* and *S. monticolus*) and weasels.

Population Parameters

Population parameters investigated in this study were density, recruitment, proportion of population

in breeding condition, probability of survival, growth parameters including mean adult body weight and juvenile growth rate, and species diversity was measured as a community attribute. Most of the parameters studied were estimated for three periods: pre-sludge summer 1990 (May-October), post-sludge winter 1990-1991 (November-April), and post-sludge summer 1991 (May-October).

Population densities were estimated by the Jolly-Seber (J/S) method (Seber 1982). Minimum number of animals known to be alive (MNA) (Krebs 1966) was calculated for those trapping periods where the J/S estimator became unreliable and impossible to calculate because of low recaptures of previously marked animals (Krebs et al. 1986). Density values were estimated for each trapping period for the three numerically dominant small mammal species: the deer mouse, Oregon vole and Townsend chipmunk. Recruits, defined as the number of new animals joining the population, were calculated from observed numbers as a cumulative value for two periods: pre-sludge (summer 1990) and post-sludge (summer 1991). The winter of 1990-91 was omitted from this analysis as no equivalent period in 1991-92 was available for comparison.

Average survival rates (J/S) were calculated for each period for males and females in control and treatment populations of both the deer mouse and Oregon vole. Survival values for chipmunks exhibited large variation in J/S values, and therefore were not used in this analysis. Early juvenile survival, defined as the percentage of observed juveniles/expected number of juveniles, was calculated for the deer mouse and Oregon vole. Expected number of juveniles was the product of the number of successful pregnancies (based on consecutive captures of lactating females) and the average number of juveniles per litter as recorded in the literature: 4.5/litter for the deer mouse (Sheppe 1963, Sadleir 1974): 3.2/litter for the Oregon vole (Gashwiler 1972). The observed number of juveniles was obtained from field data using weight as the defining parameter (deer mouse: < 17 g, Oregon vole: < 20 g.

Adults were separated from juveniles by their weight and reproductive condition. Only male weights were considered during the summer seasons because female data were complicated by undetected pregnancies. Growth rates were considered as an indicator of condition in these small mammals. Instantaneous growth rates (per day) were calculated for all juvenile animals (males and females) for periods 1 and 3 when young animals were actively growing. As growth rate is dependent on body weight, an ANCOVA of growth rate regressed on body weight was done for juvenile deer mice. Temporal (pre-vs. post-sludge periods) and spatial (control vs. treatment sites) comparisons were then made. Only deer mice had a sufficient sample size for this analysis.

Species Diversity and Richness

The Shannon-Wiener index of diversity (Pielou 1966) was used to consider both evenness and species richness in our small mammal communities. A *t*-test (Magurran 1988) allowed community indices to be compared. This index is sensitive to changes in rare species (Peet 1974). Values for the calculation of Shannon-Wiener indices were obtained from J/S estimates for the three common species. The numbers of individuals captured were used for the less abundant species: shrews, weasels, red-backed voles, jumping mice and shrew-moles. Species richness was measured by the total number of species sampled (Krebs 1989).

Statistical Analysis

A Wilcoxon paired sample test (Zar 1984) was used to compare populations over time for data that were not completely independent (the same animals were often captured during consecutive trapping periods). A Chi-square analysis was used to compare proportion of breeding animals between paired control and treatment populations. Because some samples were not completely independent, these comparisons were used as an indication of the degree of difference between sets of data. Due to low sample size, the one-tailed Fisher Exact test was used for the analysis of the proportion of Townsend chipmunks reproducing in control and treatment sites (Zar 1984). A Chi-square test was also used to detect significant differences in number of recruits and juvenile survival in control-treatment pairs between pre- and post-sludge periods. Detection of significant differences in survival and body weights between control and treatment populations was done with average values and 95% confidence limits. In all statistical analyses, the level of significance was at least $P = 0.05$.

Sludge Application

Anaerobically-digested sludge was obtained from the Annacis Island Sewage Treatment Plant in Delta, B.C. Truckloads of sludge were transported to the Research Forest and stored in a waterproof container located as close to the actual application site as possible. Prior to application, a tractor fitted with an agitator mixed the sludge to a uniform consistency. This slurry was then pumped into trash hoses (10-cm diameter) and onto the site. The total area treated was 3.58 hectares. Sludge application only partially covered treatment grids. The total amount of sludge applied was 173,823 kg (22% solids) of which the average nitrogen content was 3.9%. Variation between applications was monitored by periodic collection and analysis of sludge samples for nitrogen content. An estimated average of approximately 500 kg N/ha was applied to the sites (Kimmins et al. 1992). Sludge application began on November 25 and was completed on November 30, 1990.

Results

Trappability

The enumeration of small mammals is based on the assumption that most individuals are captured in a given population. Jolly-Seber trappability (Krebs and Boonstra 1984) was generally high for deer mice (71-91%), but variable for Oregon voles (57-77%) and chipmunks (33-75%).

Abundance and Recruitment

Fluctuations in population density of deer mice showed opposite trends for the control-treatment pairs during summer 1990 (Fig. 1A, Table 1). Numbers of deer mice were similar between control-treatment pairs in winter 1990-91 with significantly more (1.3 to 2.4 times) *P. maniculatus* on treatment than control sites in the post-sludge summer 1991. Oregon vole populations increased steadily through the late summer and fall of 1990 on both control sites with a significant difference (Wilcoxon) from those populations on pre-treatment sites (Fig. 1B, Table 1). This difference continued in summer 1991 after a similar number of voles occupied control and treatment sites in winter 1990-91. Average abundance of voles was 2.4 to 4.6 (1990) and 1.5 to 2.2 (1991) times higher on control than treatment sites. Abundance of chipmunk populations showed no difference between control-treatment pair 1, but there were significantly higher (1.7 (1990) to 4.7 (1991) times) numbers on the treatment than control site of pair 2 (Fig. 1C, Table 1). Comparison of recruitment between control-treatment pairs for pre- and post-sludge summer periods was similar for the three common species (Fig. 2).

Reproduction and Mortality

No significant differences were found for the Oregon vole in spatial (control vs. treatment) and temporal (pre- vs. post-sludge) comparisons in the proportion of animals in breeding condition (Table 2). However, this parameter was found to have increased significantly ($P < 0.01$) on treatment site 1 for both male deer mice and Townsend chipmunks (low sample size) between pre- and post-sludge periods. This increase was not observed on control sites. Significant increases in the proportion of females in breeding condition were found for deer mice in post-sludge periods for all four populations (Table 3).

There were no significant differences in average survival for either sex of deer mice or Oregon voles. Estimates of Townsend chipmunk survival values were too variable for analysis. Changes in number of successful pregnancies were similar in control and treatment populations of deer mice and Oregon voles in both pre- and post-sludge periods (Table 4). There were no significant differences in percentage (obs/exp) survival of juvenile animals between control and treatment populations, nor between pre- and post-sludge periods (Table 4). Sample sizes for the Townsend chipmunk were too low for evaluation of juvenile survival.

Growth

Average weights of adult males were not different (overlapping 95% confidence limits) between control and treatment populations for temporal and spatial comparisons for the deer mouse, Oregon vole, and Townsend chipmunk. This was also true for adult female deer mice in the winter of 1990-1991 where sample size was appropriate.

A significant difference was found in growth rate of juvenile deer mice in treatment populations after sludge application. Mean growth rate per day for the post-sludge period was almost three times that of the pre-sludge period ($F_{1, 181}=11.43$,

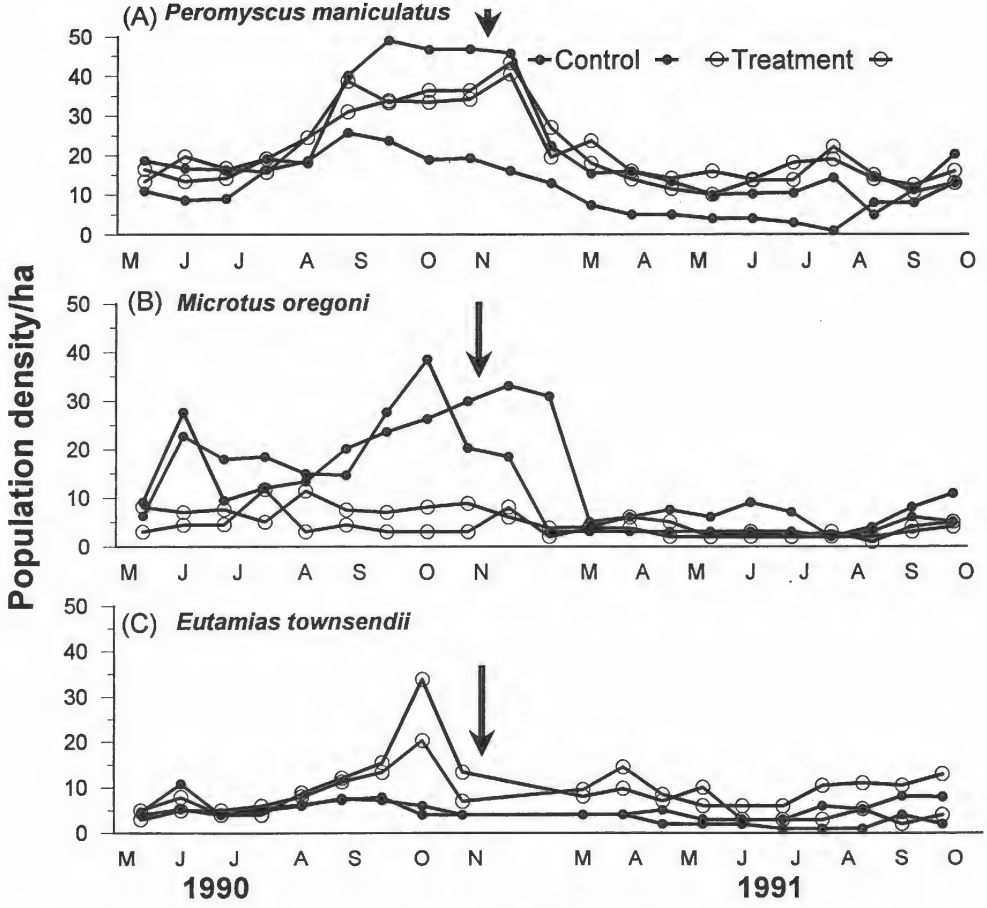

Figure 1. Population density (per ha) of (A) *P. maniculatus*, (B) *M. oregoni*, and (C) *E. townsendii* on paired control-treatment study sites. Vertical arrow indicates when sludge was applied to treatment areas.

TABLE 1. Summary of Wilcoxon Matched-Pairs Signed-Ranks Tests comparing abundance of the three small mammal species in the paired control-treatment sites. C = control, T = treatment. Number of trapping periods in parentheses.

C-T pair and period	*P. maniculatus*		*M. oregoni*		*E. townsendii*	
	C vs T	*P*	C vs T	*P*	C vs T	*P*
Pair-1						
Summer 1990 (9)	C > T	0.05	C > T	0.008	C = T	0.09
Winter 1990-91 (4)	C = T	1.00	C = T	0.47	—	—
Summer 1991 (8)	T > C	0.05	C > T	0.02	C = T	0.69
Pair-2						
Summer 1990 (9)	T > C	0.01	C > T	0.008	T > C	0.03
Winter 1990-91 (4)	C = T	0.07	C = T	0.11	—	—
Summer 1991 (8)	T > C	0.02	C > T	0.02	T > C	0.01

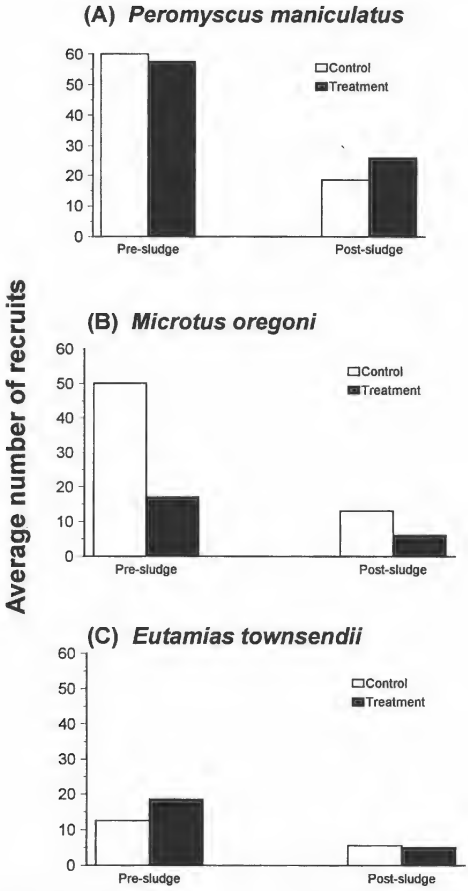

Figure 2. Average number of recruits (per ha) of (A) *P. maniculatus*, (B) *M. oregoni*, and (C) *E. townsendii* on paired control-treatment study sites during pre-sludge (summer 1990) and post-sludge (summer 1991) periods.

$P<0.01$). All other temporal and spatial comparisons were found to be not significant (Table 5).

Species Richness and Diversity

Species richness of small mammal communities on control and treatment sites averaged 6.5 and 7.5, respectively, in the pre-sludge period, and 6.0 and 6.0, respectively, in the post-sludge period. Species diversity (H') of small mammal communities on control and treatment sites was 1.57 and 1.58, respectively, in the pre-sludge period, and 1.76 and 1.48, respectively, in the post-sludge period. There were no significant differences between temporal and spatial comparisons for this diversity measurement.

TABLE 2. Proportion of adult males of the three common species in breeding condition during summer pre-sludge (1990) and post-sludge (1991) periods. Sample size in parentheses.

	Pair-1		Pair-2	
	Control	Treatment	Control	Treatment
P. maniculatus				
1990	0.41 (104)	0.33 (95)[a]	0.36 (69)	0.35 (92)
1991	0.42 (31)	0.60 (45)[a]	0.40 (25)	0.33 (51)
M. oregoni				
1990	0.30 (37)	0.67 (9)	0.34 (59)	0.67 (27)
1991	0.27 (11)	0.83 (6)	0.35 (23)	1.00 (4)
E. townsendii				
1990	0.12 (17)	0.15 (34)[b]	0.37 (19)	0.07 (27)
1991	0.00 (10)	0.75 (4)[b]	0.00 (7)	0.13 (8)

a-a, $P<0.01$; values are significantly different by chi-square. b-b, $P<0.01$; values are significantly different by the one-tailed Fisher Exact test.

TABLE 3. Proportion of adult females of the three common species in breeding condition during summer pre-sludge (1990) and post-sludge (1991) periods. Sample size in parentheses.

	Pair-1		Pair-2	
	Control	Treatment	Control	Treatment
P. maniculatus				
1990	0.33 (49)[a]	0.27 (52)[b]	0.15 (39)[c]	0.29 (48)[d]
1991	0.92 (26)[a]	0.65 (31)[b]	0.60 (10)[c]	0.77 (22)[d]
M. oregoni				
1990	0.53 (30)	0.67 (6)	0.32 (19)[e]	0.40 (15)
1991	0.67 (3)	0.33 (3)	0.86 (14)[e]	0.60 (5)
E. townsendii				
1990	0.00 (9)	0.00 (7)	0.46 (13)	0.05 (21)[f]
1991	0.40 (5)	0.33 (3)	1.00 (2)	0.29 (14)[f]

a-a, b-b, c-c, d-d, e-e, $P<0.01$; f-f, $P<0.05$; values followed by the same letter are significantly different by chi-square.

Discussion

Application of sewage sludge could potentially affect the population dynamics of small mammals in a forest environment. However, based on our results, it would appear that there was no major effect attributable to sludge treatment on population parameters one year after application. These

TABLE 4. Successful pregnancies during breeding seasons and expected (exp) and observed (obs) numbers of juveniles recruited into paired control-treatment populations up to 6 weeks after breeding for *P. maniculatus* and *M. oregoni* in pre-sludge (1990) and post-sludge (1991) periods.

C-T pair and period	*P. maniculatus*				*M. oregoni*			
	SP	Exp	Obs	% JS[a]	SP	Exp	Obs	% JS[a]
Pair-1								
Control								
1990	13	58.5	42.0	71.8	15	48.0	41.0	85.4
1991	14	63.0	28.0	44.4	4	12.8	6.0	46.9
Treatment								
1990	11	49.5	29.0	58.6	4	12.8	4.0	31.3
1991	15	67.5	24.0	35.6	2	6.4	4.0	62.5
Pair-2								
Control								
1990	6	27.0	21.0	77.8	10	32.0	30.0	93.8
1991	7	31.5	14.0	44.4	10	32.0	15.0	46.9
Treatment								
1990	10	45.0	28.0	62.2	7	22.4	15.0	67.0
1991	14	63.0	29.0	46.0	3	9.6	5.0	52.1

[a]Percentage juvenile survival (obs/exp)

TABLE 5. Mean instantaneous relative growth rate (per day) of juvenile deer mice per period and ANCOVA of growth rate regressed on body weight for the deer mouse. ** $P < 0.01$.

Comparison	Mean instantaneous relative growth rate ($\times 10^{-3}$)	*F*	*P*
Pre-control vs. Post-control	2.7 3.7	0.32	0.75
Pre-treatment vs. Pre-control	2.3 2.7	0.40	0.59
Post-treatment vs. Post-control	6.1 3.5	1.26	0.27
Pre-treatment vs. Post-treatment	2.3 6.1	11.43	0.0009**

parameters included abundance, reproduction, survival, growth and species diversity. Growth rate of juvenile deer mice increased significantly after sludge treatment.

Small Mammal Populations

Annual and multi-annual population fluctuations in abundance of small mammals are not unexpected and have been well documented in the literature for *P. maniculatus* (Sadleir 1965, Healey 1967) and *M. oregoni* (Gashwiler 1972, Petticrew and Sadleir 1974, Hooven and Black 1976) and were evident on all study areas. The low abundance of control populations in 1991 suggests that small mammal populations were at a low point in their fluctuation rather than their low numbers being a result of sludge treatment. Declines in Oregon vole abundance on all sites were attributed to the characteristic 3- to 4-year fluctuations of this species (Gashwiler 1972, Hooven and Black 1976, Sullivan and Krebs 1981a) with the 1991 data covering a presumed decline in vole abundance.

The observed increase in Oregon vole recruitment during periods of reduced deer mouse recruitment may have been related to competitive interactions between the two species. Data collected from these sites during a previous study supports this possibility (Sullivan 1990b). Interspecific competition has also been previously recorded for these two species in a young plantation (Petticrew and Sadleir 1974). Moreover, voles of the genus *Microtus* have been shown to competitively exclude deer mice from grassland areas (Grant 1971, Redfield et al. 1977).

Data from this study indicate that the deer mouse appeared to not be negatively affected by the sludge treatment as illustrated by its high survival and reproductive attributes. This is reinforced by the work of Petticrew and Sadleir (1974) and Sullivan (1979) which concluded that there was little

variation in demographic parameters of deer mouse populations in different habitats of coastal forests.

The increase in growth rate of deer mice on treatment sites suggests that fertilization effects from sludge may have caused an increase in growth of juvenile deer mice by increasing the nutrient content in the plant products associated with treated vegetation. Increases in nitrogen and phosphorus were also found in salal foliage in the post-treatment year (Coward 1993). The increase in the mean growth rate of juvenile deer mice found on treatment sites in 1991 did not affect this species' abundance, survival, recruitment or average adult weight. This may be due to short-term effects of the initial sludge application. The timing of the application may have also contributed to a limited effect. Sludge was applied in late November when deciduous vegetation was in senescence. More extensive effects may have occurred if sludge was applied in the midst of summer when both small mammals and ground vegetation were actively growing.

Other studies investigating the effects of sewage sludge on small mammals have variable results. Hegstrom (1986) found no response in abundance of shrews to sludge treatment although insectivores had higher levels of cadmium in their livers and kidneys after treatment. Conversely, West et al. (1981) found populations of herbivorous rodents (*M. townsendii, M. oregoni* and *C. gapperi*) were significantly lower in density on treated than control sites, presumably due to changes in plant species composition which acted as food and cover for this group. Their study, however, was based on data from one trapping period of four days in duration and lacked temporal controls.

Habitat Alteration

Studies on the response of small mammals to forest herbicide use showed no significant effect on their population parameters (Sullivan and Sullivan 1981, 1982, Sullivan 1990a). Conversely, a definite effect has been observed for clear-cut logging and burning. Sullivan and Krebs (1981b) found an irruption in the number of deer mice in an old-field habitat adjacent to a forest immediately after the forest was harvested by clearcutting. This increase in recruitment was not recorded in the study site in the logged area. Sullivan and Boateng (1996) reported a significant decrease in abundance of deer mice shortly after a prescribed burn on a clear-cut site as compared to a control area.

Relative to other habitat alteration practices, silvicultural sludge applications are expected to have less impact on small mammal populations than logging or burning. In sludge applications, vegetation is not altered as intensely as in a herbicide application or a clear-cut logging operation. In addition, fertilization effects of the sludge may enhance some vegetation after treatment (Sullivan and Rochelle 1992, Coward 1993). Consequently, the impacts on small mammals which utilize this vegetation as food and habitat would likely not be as great as in other forestry practices. Other wildlife groups, however, may not be as adaptable. Insectivores (such as shrews), ground nesting birds, and amphibians are a few groups that may be sensitive to the sludge application.

Study Limitations

Improvements in the experimental design include increasing the number of replicates, as well as the scale, and duration of application. Only two sites were treated with sludge in this study as part of the overall project design. Moreover, sludge was applied to only part of the treatment grids. A minimum of three replicates is recommended in future studies. Application on a larger scale (e.g. 5-10 ha) is also suggested. Sludge applications in the size range of this study may be too small to significantly impact mobile small mammals such as the deer mouse and chipmunk. These generalist species may be able to modify their behaviour and territories to adjust to sludge treatment relatively easily when the area treated is small. Operational applications are likely to be of much larger scale.

Future studies could apply sludge in the middle of the summer season when vegetation and small mammals are actively growing. Parameters such as reproduction, growth and recruitment are best observed then. The application of sludge in this study took place in late November and this timing may have contributed to the limited effect observed. However, this was a realistic time of application from an operational perspective and the study results should be evaluated accordingly. Lastly, increasing the duration of this study to three or five years post-treatment may reveal long-term effects on population dynamics not exhibited in a short-term study.

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On the Holocene History of Elk (*Cervus elaphus*) in Eastern Washington

Abstract

Historically, North American elk (*Cervus elaphus*) were thought to have been absent from the arid steppe habitats of the Columbia Basin of eastern Washington. McCorquodale (1985, *Northwest Science*) used zooarchaeological data to show elk had been present there during the Holocene. Presently available zooarchaeological data indicate elk were present during each 1000 yr increment of the last 5000 years, but those data are not sufficiently robust to allow detection of changes in the range or abundance of elk. Limited data suggest that the introduction of Euroamerican technology and horses to Native American peoples may have initiated local extirpation of late prehistoric–early historic elk, and that some late-prehistoric elk in the Pacific Northwest were larger than modern elk.

Introduction

Since the middle of the nineteenth century when Suckley and Gibbs (1860:133) wrote that they "suppose[d] that the range of the [North American wapiti or elk (*Cervus elaphus*)] from the Rocky Mountains to the Pacific has been by the line of the heavily timbered Cascade Mountains," many researchers have believed that elk did not occur in the relatively arid steppe habitats of the Columbia Basin of eastern Washington state (Bailey 1936; Dalquest 1948; Murie 1951; Bryant and Maser 1982). Historic literature largely fails to provide evidence to the contrary (e.g., Schullery 1984), and suggests that elk were never very abundant east of the crest of the Cascades. Thus, McCorquodale (1985:192) cautioned that "an assessment of the original distribution of elk based upon these sources must be considered suspect."

McCorquodale (1985) turned to the zooarchaeological record to study the original occurrence of elk in the Columbia Basin. Citing data from just over a dozen archaeological sites, he found that the available evidence did "not support the hypothesis that elk were not present in the Columbia Basin" and concluded that they had been present during the Holocene or last 10,000 years (McCorquodale 1985:196). In this paper we expand on McCorquodale's (1985) analysis using his data as well as data gathered in the decade since his paper was published. In undertaking this analysis, we sought to refine McCorquodale's conclusions by searching for changes in the distribution of elk through time. We attained only limited success in this endeavor due to limitations of the available sample, but found no evidence to contradict his findings.

The Columbia Basin

We define the Columbia Basin as that area of eastern Washington bordered on the west by the Columbia River, on the north by the Columbia and Spokane rivers, on the east by the edge of coniferous forests (just west of or approximating the Washington–Idaho border), and on the south by the Snake River (Figure 1). This area is relatively arid with warm to hot summers and cool winters. Vegetation is characterized as steppe and is dominated by big sagebrush (*Artemisia tridentata)* and bunchgrass (*Agropyron* sp., *Festuca* sp.)(Daubenmire 1970). The Columbia Basin is surrounded by coniferous forests consisting of various tree species (Franklin and Dyrness 1973). In order to gain as full an understanding as possible of the biogeographic history of elk, we defined our study area as that part of Washington east of the crest of the Cascade Mountains and within the northern, eastern, and southern boundaries of that state.

Fossil pollen and mammal remains suggest the post-glacial Holocene geological epoch was dominated by steppe vegetation and mammalian taxa (e.g., Lyman and Livingston 1983; Whitlock 1992). However, there were significant changes in climatic patterns during the Holocene that resulted in changes in habitat and in distributions of some mammalian taxa (e.g., Lyman 1991; Lyman and

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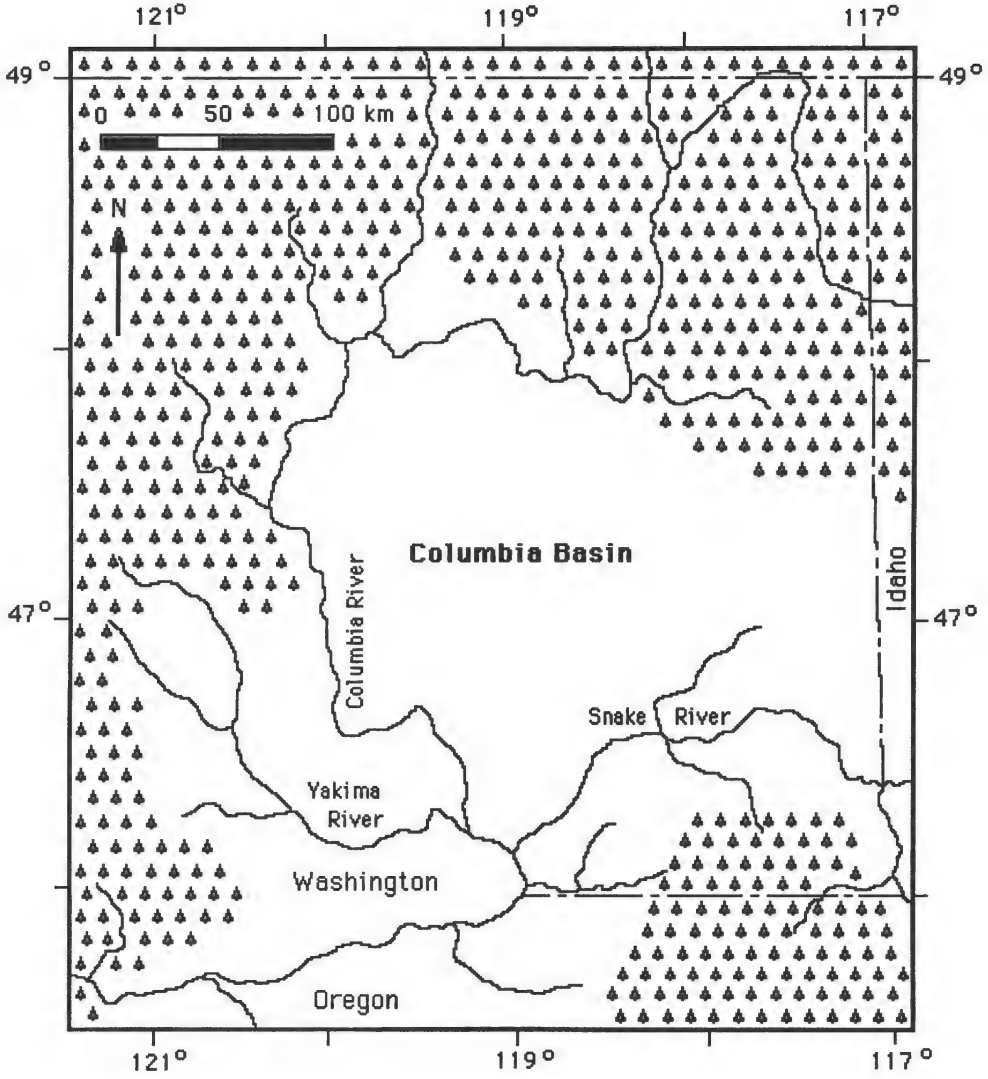

Figure 1. Distribution of forest habitats in eastern Washington (after Daubenmire 1970).

Livingston 1983). Thus, a single map showing archaeological sites that have produced remains of elk, but that disregarded the age of those remains, would not reveal potentially significant details of the biogeographic history of this species.

Historic data (e.g., Schullery 1984) indicate elk were seldom found in the central arid Columbia Basin after 1850. Elk tended to be restricted to timbered habitats surrounding the basin during the late nineteenth and early twentieth century (Bryant and Maser 1982; Ingles 1965; Peek 1982; Figure 2). Only in the last twenty years or so have elk begun to move out of the forests into the steppe habitats of the western portion of the basin (e.g., Rickard et al. 1977) where a small population has become established (e.g., McCorquodale 1993 and references therein). This historic event underscores the possibility that elk may have at some time in the past

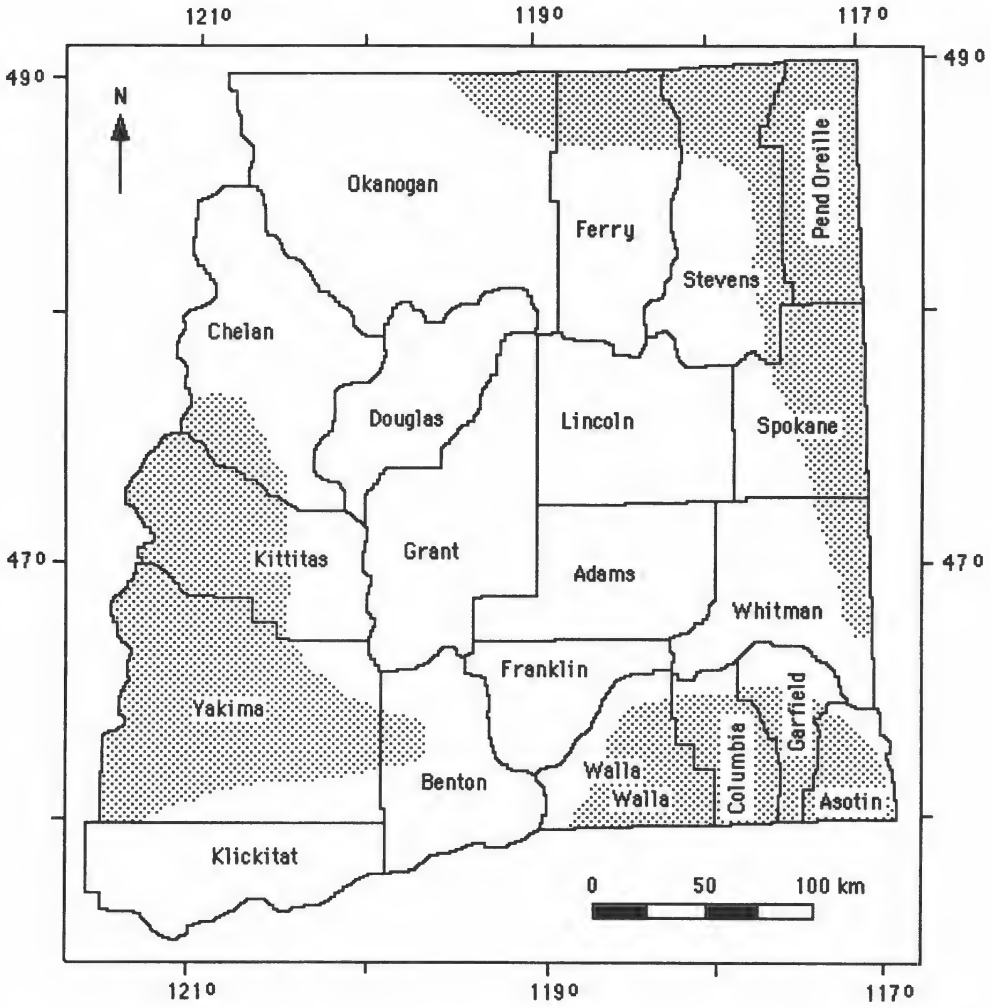

Figure 2. Approximate modern distribution of elk (stipled) in eastern Washington (after Booth 1947; Dalquest 1948; Ingles 1965; with modifications). County lines and names shown for reference.

been much more widespread in eastern Washington than during the previous 100–200 years.

Methods and Materials

We examined published and unpublished archaeological reports for evidence of elk. (Virtually no Holocene-aged paleontological mammalian remains have been reported in the area.) When an archaeological site had produced such remains, we recorded (a) the frequency and kinds of elk skeletal parts recovered, (b) stratigraphically associated radiocarbon dates, (c) where the site was located, (d) when the site was excavated, and (e) when the faunal remains were reported. The first attribute helped us determine if the remains were of local derivation or if they might have been traded or transported into the site from elsewhere (see Lyman 1994 for a review). The last two variables allow us to assess sample adequacy and validity for determining changes in the prehistoric distribution of elk through time.

Stratigraphically associated sets of elk remains—assemblages—were assigned a chronometric age if they had one or more associated radiocarbon dates. In those cases when more than one radiocarbon date was available for an assemblage, we calculated the simple average of the multiple dates, and used that average to assign the assemblage a chronometric age. All assemblages with a chronometric age were assigned to one of six arbitrary time periods. Five of these span 1000 year periods, beginning with 0–1000 yr BP (radiocarbon years Before Present) and ending with 4000–5000 yr BP. The sixth time period spans the first half of the Holocene—5000–10,000 yr BP—because there were so few dated assemblages falling in this time span that to distinguish shorter time periods would have provided no useful information for our purposes.

We drafted a map for each of the six time periods, plotting the locations of sites that produced dated elk remains on the appropriate map. We also plotted all undated occurrences of elk on the 5000–10,000 yr BP map. Study of these maps (Figure 3) suggests where elk were at particular times in the past, but, as we will show, the maps tell us little about where elk were not present in the past.

Results

Seventy-seven archaeological sites in eastern Washington have produced over 1300 skeletal remains of elk. The latter value is a minimum because frequencies of elk remains were seldom reported prior to 1970; early reports rarely even note the presence of elk or other faunal remains. Fifty sites containing 74 assemblages of elk remains have been chronometrically dated; 35 additional assemblages have not been so dated or are dated to periods significantly exceeding a 1000-year time span and thus cannot be easily placed within one of our time periods.

A composite map of all dated and undated sites suggests that elk were present throughout eastern Washington, if at different times in different places, during the Holocene. Maps of the dated assemblages (Figure 3) indicate elk were rather consistently present throughout the Holocene in the upper-middle Columbia River area—between Okanogan and Douglas counties—and along the lower Snake River of southeastern Washington. Were elk in fact more regularly present in these two areas relative to other areas? We believe this question cannot be answered with the available data for two reasons.

First, zooarchaeological research—which we define as the detailed description of animal taxa represented and their abundances in collections recovered from archaeological sites—only began to be systematically accomplished in eastern Washington in the 1970s (e.g., Gustafson 1972; Deaver 1973; Lyman 1976). Much of the archaeological research in the area, however, took place between 1950 and 1980 as a result of hydroelectric projects along the Columbia and Snake rivers. Thus, several rather large archaeological projects—such as those upstream of McNary Dam (Osborne 1957; Shiner 1961), Priest Rapids Dam (Greengo 1986), Wanapum Dam (Nelson 1969; Swanson 1956, 1962), Rock Island Dam (Hartman 1975), Rocky Reach Dam (Gunkel 1961), and Wells Dam (Grabert 1968) on the Columbia, and Ice Harbor Dam (Grater 1966; Rice 1965) on the Snake—resulted in the generation of much archaeological data but minimal, typically not detailed, and often undated zooarchaeological data. Later projects behind some of these and other dams—such as Wells Dam (Chatters 1986), Chief Joseph Dam (Campbell 1985), and Grand Coulee Dam (e.g., Chance and Chance 1985) on the upper-middle Columbia—have filled some of these gaps.

The second reason for the geographic gaps is that radiocarbon dating—the chronometric technique typically employed by archaeologists in eastern Washington—while first used in eastern Washington in the 1950s, was not consistently used until the 1970s, and even then not all assemblages of artifacts or faunal remains were dated. Thus, we not only have elk remains from sites excavated prior to 1950—such as those upstream of Grand Coulee Dam recovered in the 1930s (e.g., Collier et al. 1942)—that have no associated radiocarbon dates, we also have elk remains from sites excavated in the late 1950s with no associated radiocarbon dates—such as those in the Rocky Reach Dam reservoir area (Gunkel 1961).

To assess the influence of the history of archaeological research on the available zooarchaeological data, we compared two pairs of variables. In the first comparison, one variable is the date when a site producing elk remains was first reported; the second variable is the date when a site—whether or not it produced remains

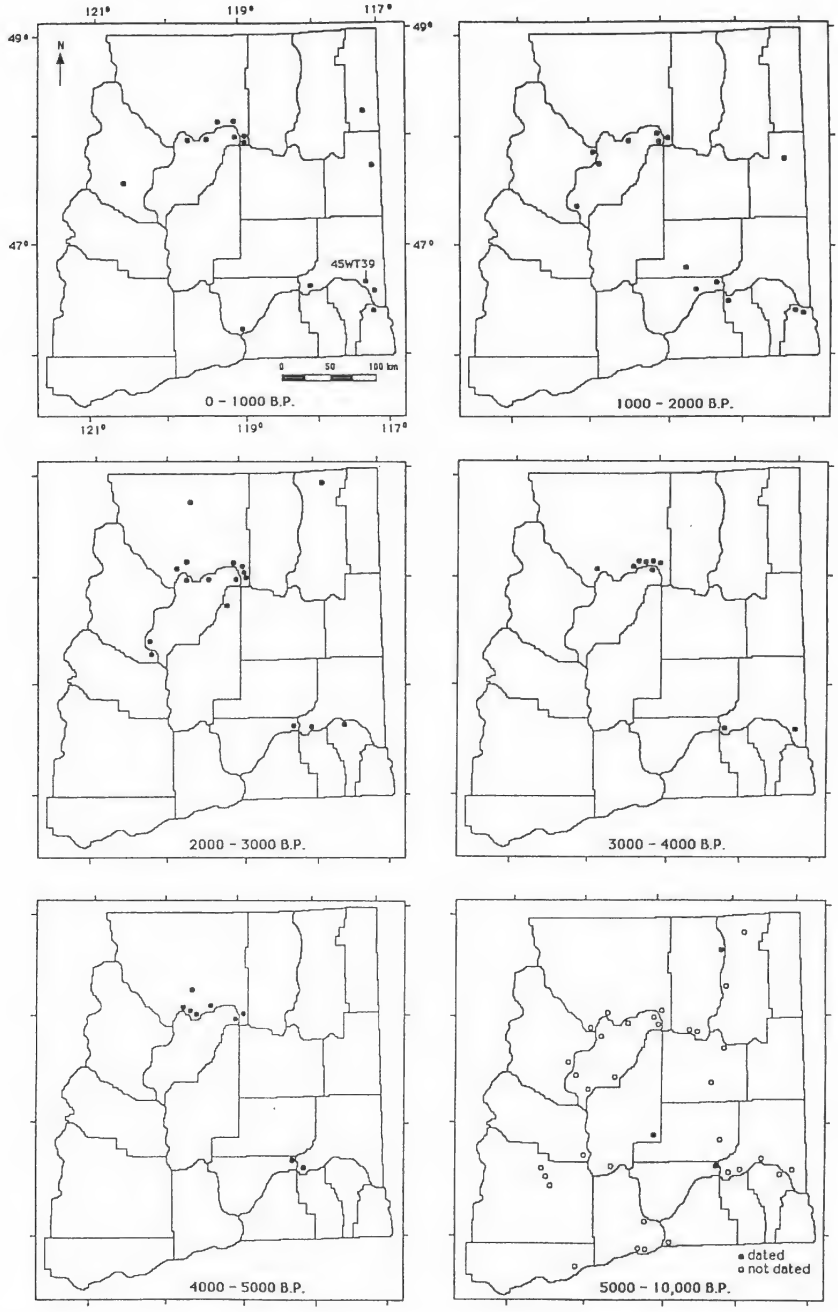

Figure 3. Distribution of sites producing elk remains per thousand year period; county lines shown for reference.

of elk—was first dated via radiocarbon analysis. We tallied the number of sites per five year increment, beginning with those reported prior to 1950. The two variables are correlated (Spearman's rho = .87, P = .002), as implied in Figure 4. But note that between 1955—the beginning of the period when the first site was radiocarbon dated—and 1964, the number of sites reported to have produced elk remains exceeds the number of dated sites. After 1964, the number of dated sites—with one exception, 1970-74—exceeds the number of sites reported to have produced elk remains in all 5-year periods. This bivariate comparsion, then, suggests that the history of reporting elk remains has been somewhat different than the history of dating archaeological sites and their included faunal remains.

In the second comparsion, we tallied the number of dated assemblages per county irrespective of the age of the assemblage. Results (Figure 5) indicate that 44 of the 74 total dated assemblages are found in two counties—Douglas and Okanogan. Twenty dated assemblages are found in counties adjacent to the lower Snake River in southeastern Washington. Thus, 86% of the dated assemblages are found in these two areas; that is, well over three-fourths of the dated assemblages are from less than half—8 of 20—of the total counties. Clearly, the data available are not evenly distributed geographically. The distribution maps (Figure 3) seem, then, to tell us more about when and where post-1970 zooarchaeological research has been done than where elk were not to be found during the Holocene.

The maps do, however, indicate to some degree where elk were during the Holocene. Artifacts of elk bone and antler have been found in many archaeological sites, but those sites have also produced non-artifactual bones and teeth of individual elk that were very probably taken within a few kilometers of where the remains were found. This seems likely because all portions of the skeleton—some that might have been transported long distances as well as many that probably were not transported long distances due to their low value as a source of food or tool material to prehistoric humans—are regularly represented when the sample exceeds a dozen or so specimens. Thus, we suspect the maps indicate well some of the places where elk were found during the last half of the Holocene.

Three sites have each produced over 90 bones and teeth of elk. Only one of these has been dated via radiocarbon analysis, but it is just across the Snake River from one of the other two. These two nearly contiguous sites—45WT39 (Yent 1976; see Figure 3a) and 45GA61 (Lyman, unpublished data)—seem to date to the same time period—the

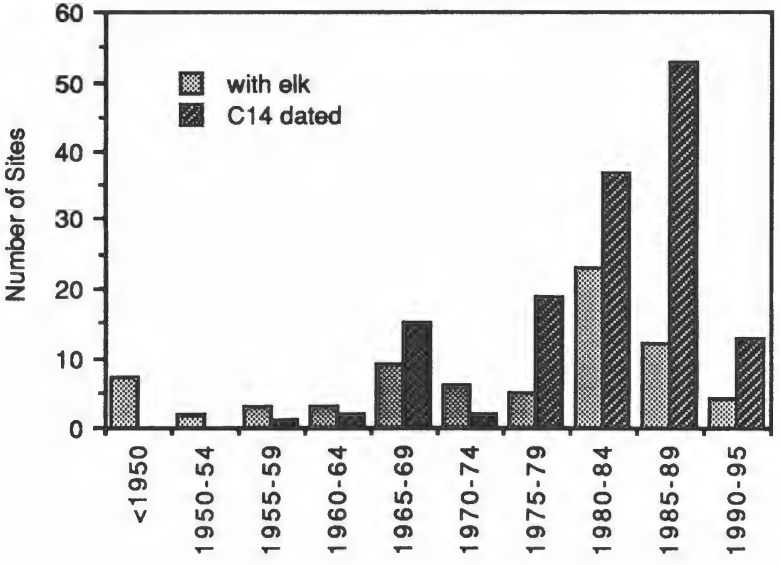

Figure 4. Frequency of sites producing elk remains and frequency of dated sites per five-year period.

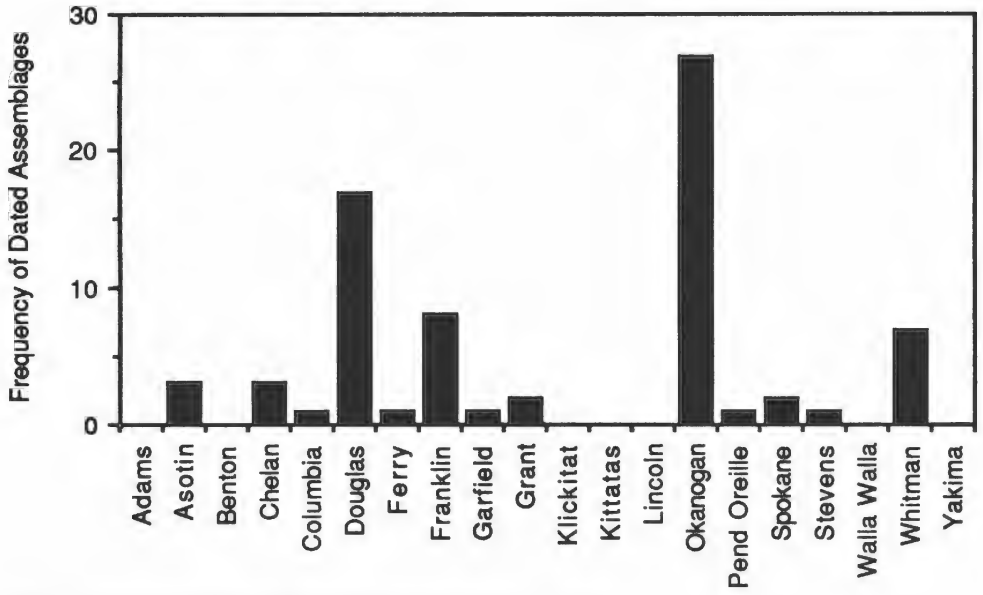

Figure 5. Frequency of dated assemblages producing elk remains per county.

last 1000 years—based on similarities of artifact styles. Together these two sites suggest that elk may have been abundant here relative to other areas of eastern Washington in the recent past—elk remains make up ≥28% of the artiodactyl remains from these two sites, but tend to have lower relative abundances in most other assemblages we have examined. The other site with numerous elk remains is in Ferry County (Collier et al. 1942).

Discussion

Couch (1935:4) suggested that "it is not known if the Rocky Mountain wapiti (*C. e. nelsoni*) formerly inhabited any areas in eastern Oregon and Washington prior to [their] introduction [early in the twentieth century]," but he also went on to suggest "No doubt this species was originally in [eastern Washington but] with the arrival of man and subsequent settling of the country, the elk were practically exterminated in the Cascade region and the eastern portion of the two states." We suspect Couch is referring to Euroamerican settlers of the nineteenth century rather than the late Pleistocene settlement of the area by Native Americans. Booth (1947:571) indicated that the Rocky Mountain elk "likely ranged formerly over most of the eastern part of [Washington] state, but then was exterminated." Murie (1951:20) stated that it "appears [that much of the arid portion of eastern Washington has] been unoccupied by elk." Bryant and Maser (1982:57) noted that "controversy still exists as to [the elk's] past occurrence on the east slope of the Cascade Mountains" of Washington.

While limited, the data we have compiled (Figure 3) indicate that it is probable that elk did occur on the eastern slope of the Cascades in the past. Further, these data suggest that elk were rather more widespread across eastern Washington prior to the nineteenth century than later. Did Euroamerican settlement result in the extirpation of eastern Washington elk populations? Perhaps (e.g., Edson 1930, 1931; Schullery 1984), but the introduction of horses and firearms to Native American groups in the eighteenth century may have initiated the extirpation process (Schalk 1980). In his review of historic data concerning the Mt. Rainier area just to the west of the southern half of our study area, Schullery (1984:23) found that early nineteenth century Euroamericans were surprised by the paucity of big game and "were inclined to attribute those low numbers to overhunting by tribes in the area." A similar explanation for the rarity of big game in the Mt.

Baker area to the west of the northern half of our study area was offered by Brooks (1930) but was disputed by Edson (1930, 1931) who felt Euroamerican hunters were to blame. The potential impacts of Native American hunters on big game populations have become increasingly clear in the last decade, and their relevance to modern wildlife management issues are only now becoming understood (e.g., Kay 1994). The effect of such hunting on eastern Washington elk populations is presently unclear.

Taber et al. (1982:289) report that "transmission of disease from domestic livestock [applied] new pressures to elk populations." Kistner (1982) lists several bacterial diseases and some parasites have been transmitted from domestic livestock to elk. The impact of such exotic pressures on eastern Washington elk is probably irrelevant to determining late eighteenth century population sizes because it was not until the middle of the nineteenth century that the livestock industry began to flourish (Oliphant 1948). Exotic diseases introduced by Euroamericans may, however, have had an indirect impact on elk populations. As the Native American population became infected with European human diseases it decreased an estimated 30% by 1800, and 50% by 1830 (Boyd 1990). Resulting disruption to native cultures was significant; many traditional practices were discontinued (Dunnell 1991). One such discontinued practice was burning vegetation. "Broadcast burning by native peoples of the inland Pacific Northwest was widespread and persisted over an extended period primevally" (Shinn 1980:415). Given that elk seem to proliferate in recently burned areas (Peek 1982:859), discontinuation of Native burning in the earliest nineteenth century may have contributed to declines in elk populations. Thus, in order to identify the late prehistoric–early historic forces that controlled the size of the elk population, not only must zooarchaeological data become much more spatially representative of the area, it must become more tightly controlled chronologically as well if we are to begin to sort out the effects of Native American hunting from the impacts of Euroamerican settlement on resident populations of elk and other species.

Another factor that may eventually play a role in more effective management of elk in the area is the apparent differences in size of modern and prehistoric elk populations. Fryxell et al. (1968:514) noted nearly three decades ago that late-Pleistocene-aged elk remains recovered from Marmes Rockshelter near the lower Snake River of southeastern Washington were "larger than those of living representatives in the area today," but no data have ever been presented to substantiate this observation despite more recent studies of the faunal remains from this site (e.g., Caulk 1988). Distal metapodial condyles of elk dating between 700 and 200 BP and recovered from the Meier site in the Portland Basin are (a) larger than most comparative specimens of Rocky Mountain elk (*C. e. nelsoni*); (b) overlap with but are generally larger than comparative specimens of elk killed by the 1980 eruption of Mount St. Helens (minimally, these elk are descendants of Rocky Mountain elk transplanted to the area early this century; they may be hybrid descendants of this transplanted gene pool and a native gene pool of unclear taxonomic affinity [Schullery 1984]); and (c) overlap in size with, but also have many individuals larger than, comparative specimens of Roosevelt elk (*C. e. roosevelti*; Figure 6). These and other data (Lyman, unpublished) from this and other sites in the Pacific Northwest suggest some late prehistoric elk populations in the area contained larger individuals than presently exist.

Late Pleistocene gigantism has been observed in other large mammals across the contiguous 48 states (e.g., Graham 1991; Harris and Mundel 1974; Hughes 1978; Wang and Neas 1987; Wilson 1978), but so far as we know has been reported for elk only in eastern Washington. Research on the closely related Norwegian red deer (there is some debate whether this cervid should be considered conspecific with North American elk; e.g., Schonewald 1994) indicates this animal tends to attain larger adult size in cool-dry climates than in warm-moist climates due to differences in the physiology of foraged plants (Langvatn and Albon 1986). Perhaps, then, habitat and climatic differences between the twentieth century, and times prior to the nineteenth century, produced larger elk prehistorically than historically. Such climatic differences may have placed elk resident to the Columbia Basin under selective pressure, contributing to their extirpation in some areas and their diminution in other areas. But this is conjectural because as yet we do not have sufficient, chronologically well-controlled morphometric data to map the history of late Quaternary elk diminution.

Prehistoric hunting pressure may have (a) resulted in prehistoric overkill, or (b) continually reduced intraspecific competition to the point that the elk found in the Columbia Basin and adjacent

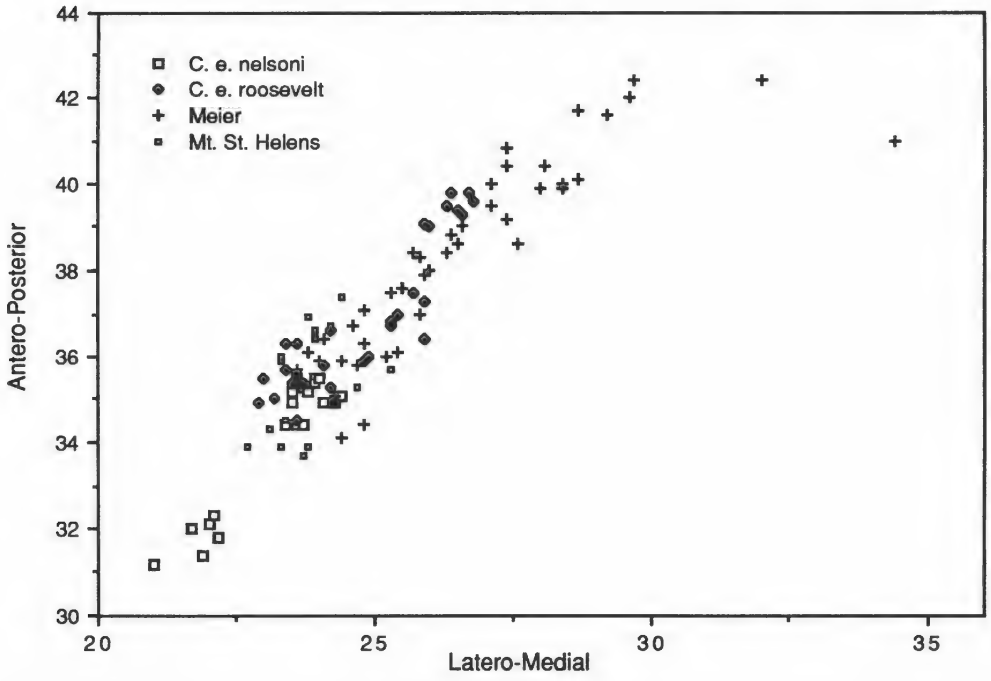

Figure 6. Latero-medial width (mm) plotted against antero-posterior breadth (mm) of elk distal metapodial condyles in three modern comparative samples and one archaeological (Meier) collection.

areas responded for extended periods of time much like a colonizing population. McCorquodale et al. (1989) found that elk historically colonizing the western portion of Benton County in Washington tend to have larger than average antlers and relatively high reproductive and survival rates. We suggest, therefore, that measures of prehistoric hunting pressure (e.g., Lyman 1987) in correspondence with morphometric analysis of tightly dated elk remains and modeling of past environmental systems (e.g., Whitlock 1992) may reveal much regarding not just the biogeographic history of elk in eastern Washington, but the ecological history of elk as well. Such analyses will allow evalution of Couch's (1935) and Booth's (1947) hypothesis that Euroamerican settlement resulted in local extirpation, and may reveal why at least some prehistoric elk in the northwest were larger than their modern relatives.

Conclusions

A decade ago McCorquodale (1985) concluded that elk had been present prehistorically in the arid steppe habitats of the Columbia Basin of eastern Washington. Subsequent research does not contradict this conclusion. Our data indicate that elk were rather consistently present there throughout the last half of the Holocene, and probably also during the first half of the Holocene. Available data do not, however, allow us to monitor changes in elk distribution because those data closely reflect the history of archaeological research in the area. Typical explanations for the absence of elk from the Columbia Basin suggest over-hunting by Euroamerican settlers resulted in local extirpation. A slowly growing body of data indicates, however, a combination of (a) technology introduced to Native Americans and (b) pre-nineteenth century climatic-induced stress may have initiated the extirpation process.

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Corrections for Position Bias of a LORAN-C Radio-Telemetry System Using DGPS

Abstract

Position estimates determined from Long Range Navigation-C (LORAN-C) can be biased because of rugged topography, power lines, and mineral deposits. We corrected position bias of a LORAN-C automated animal tracking system used on the Starkey Experimental Forest and Range in northeast Oregon to track movements of Rocky Mountain elk (*Cervus elaphus nelsoni*), mule deer (*Odocoileus hemionus*), and cattle (*Bos taurus*). LORAN-C time differences were obtained from 386 Differential Global Positioning System sites located systematically throughout the Starkey Experimental Forest and Range. We used geostatistics to interpolate position-dependent LORAN-C distortions in the Starkey Experimental Forest and Range to improve the absolute positioning accuracy of the automated animal tracking system. Time differences were obtained from LORAN-C collars placed at 20 random sites. Positions were calculated after correcting these time differences for bias. These positions were compared for accuracy against the same positions determined by a Differential Global Positioning System (accuracy level within 2-5 m, Trimble Navigation, Inc.). Positioning accuracy increased for the original automated animal tracking system ($P < 0.05$) when two corrected time differences were used to obtain positions but not in the upgraded automated animal tracking system ($P > 0.05$) when 3-4 corrected time differences were used to determine positions. However, uncorrected positions from the upgraded automated animal tracking system were as accurate as corrected positions from the original automated animal tracking system. We are 90% confident that each LORAN-C position, after correcting for bias, was within a 3.4 ha area in the original automated animal tracking system and a 3.1 ha area in the upgraded automated animal tracking system, respectively. We believe that this attained level of accuracy will be adequate for habitat studies given the size distribution of habitat polygons within the Starkey Experimental Forest and Range. Methods presented to identify and correct bias of radio-telemetry positions can also be used to increase positioning accuracy of non-LORAN-C based radio-telemetry.

Introduction

The potential of Long Range Navigation-C (LORAN-C) for wildlife research along coastal environments has been described (Patric et al. 1988, Boer et al. 1989, Collazo and Epperly 1995). Although Leptich et al. (1994) evaluated the accuracy of aircraft-based LORAN-C for wildlife research, few data are available on the terrestrial-based accuracy of LORAN-C, especially at sites in interior North America, and its usefulness for radio-tracking free-ranging wildlife.

In 1989, the automated animal tracking system was deployed on the Starkey Experimental Forest and Range (Starkey) to track positions of Rocky Mountain elk (*Cervus elaphus nelsoni*), mule deer (*Odocoileus hemionus*), and cattle (*Bos taurus*; Bryant et al. 1991, Johnson et al. 1991). This system computes positions of animals equipped with LORAN-C collars by differentially correcting the time differences of signals received by the collar and retransmitting them to the automated animal tracking system center (Dana et al. 1989). During summer and fall 1991, we placed LORAN-C receivers used to track animals at known positions computed by Differential Global Positioning System (DGPS) to determine the accuracy of the automated animal tracking system. Results of these tests showed multi-directional biases in LORAN-C positions up to 150 meters, particularly in the northwest corner of the study area (S. L. Findholt, unpubl. data). A bias of this magnitude was considered unacceptable given the distribution and size of habitat patches within Starkey and the goals of our research. Therefore, our objectives were to: (1) report on the accuracy of a terrestrial-based LORAN-C radio-telemetry system at an interior study site, (2)

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document the magnitude and extent of LORAN-C biases within Starkey, (3) develop corrections to increase position accuracy of the automated animal tracking system, and (4) evaluate the extent to which corrections improved accuracy. In this paper we used White and Garrott's (1990) definition of bias which is a mean error significantly different from zero.

Methods

Description of Study Area

The study area included most of the Starkey Experimental Forest and Range, located on the Wallowa-Whitman National Forest, about 35 km southwest of La Grande, Union County, Oregon (Figure 1). Vegetation on Starkey is a mosaic of forest stands and open areas (Strickler 1965). Forest stands are dominated by ponderosa pine (*Pinus ponderosa*), with grand fir (*Abies grandis*) and Douglas fir (*Pseudotsuga menziesii*) occurring on northern aspects. Soils are derived from basalt and pumicite (Strickler 1965). The 10,102 ha study area at Starkey is enclosed with a 2.4 m high fence that restricts movements of elk and deer. Elevation ranges from 1,120 to 1,500 m.

Magnitude and Extent of LORAN-C Bias

We used the University of Calgary's LORCAL system to determine the magnitude and extent of position-dependent biases within Starkey (Lachapelle and Townsend 1991). LORCAL is a portable system used for the signal analysis and calibration of LORAN-C using DGPS. From 25 November to 27 November 1991, approximately 20,000 data points were collected covering nearly 242 km of accessible roads within Starkey.

Differences Between Original and Upgraded Automated Animal Tracking System

Dana et al. (1989) described the original automated animal tracking system installed at Starkey. Briefly, the base station computer requests a position from the radio collar via a coded signal that activates the collar's LORAN-C receiver. LORAN-C signals received by the collar are rebroadcast by the collar over a microwave link to radio towers that relay the signals to the base station. Positioning software converts the LORAN-C signals into differentially corrected UTM coordinates and stores the results in the computer. In the original radio-telemetry system at Starkey positions were computed every 15 seconds, whereas in the upgraded system, positions are obtained every 20 seconds.

The main differences between the original and upgraded radio-telemetry systems affecting position accuracy are the number and locations of LORAN-C transmitters used by each system (Figure 1). In the original automated animal tracking system, positions were determined from three LORAN-C transmitters from the U.S. West Coast chain (Group Repetition Interval, GRI 9940) located at George, Washington (9940W), Fallon, Nevada (9940M), and Middletown, California (9940X). The upgraded system, installed on 17 July 1992, uses six LORAN-C transmitters, the original three along with three others: Searchlight, Nevada (9940Y) and transmitting towers at Havre, Montana (8290M) and Williams Lake, British Columbia (8290Y) from the North Central U.S. (NOCUS) LORAN-C chain (GRI 8290).

Corrections for LORAN-C Bias

Corrections for bias were developed for the original and upgraded automated animal tracking systems. From 24 February 1992 to 15 May 1992, a systematic sample of 372 sites was located within Starkey at approximately 400 m intervals. At each site, LORAN-C time differences were measured on 9940W and 9940X using a portable, land-based Apollo Model 602 LORAN-C receiver (II MORROW Inc., Salem, OR). After learning that the upgraded automated animal tracking system at Starkey would use data from GRI 8290 and a fourth transmitter from GRI 9940, time differences were measured at 14 random sites located throughout Starkey for 9940Y and 8290Y. Time differences obtained with the remote LORAN-C receiver were differentially corrected with data from an Internav LC408 dual-chain LORAN-C receiver at the Starkey computer center. Without differential correction, LORAN-C position error would increase by about 1,200 m at Starkey. LORAN-C time differences were measured to the nearest 0.1 micro-second (μs; i.e., 30 m).

A true position was determined for each of 386 sites at Starkey by collecting a minimum of 180 three-dimensional fixes at each site with a GPS receiver (Trimble Pathfinder, Trimble Navigation Ltd., Sunnyvale, CA). DGPS operating parameters used were an elevation mask of 15

Figure 1. Locations of LORAN-C transmitting towers in the western United States and Canada used to obtain position estimates on the Starkey Experimental Forest and Range, northeast Oregon. LORAN-C transmitting towers at Fallon (Nevada), Middletown (California) and George (Washington) were used in the original automated animal tracking system. These transmitting towers in configuration with those at Williams Lake (British Columbia), Havre (Montana), and Searchlight (Nevada) were used in the upgraded automated animal tracking system.

degrees, a signal-to-noise ratio mask of 6, position dilution of precision (PDOP) mask of 8, and PDOP switch of 6. The 180 positions were differentially corrected using data from the Pacific Northwest Region Community Base Station in Portland, OR, 319 km from the computer center at Starkey, and then averaged for a single position for each site. Base station positions were collected at 5-second intervals with a GPS receiver (Newton 6 channel, Trimble Navigation Ltd., Sunnyvale, CA). DGPS estimated positions were compared to three sites within Starkey with known locations to assess the accuracy of DGPS. UTM coordinates obtained by DGPS were converted to the appropriate time differences for each pair of LORAN-C transmitters. The differences between the differentially corrected LORAN-C and DGPS time differences represent the distortion in the LORAN-C signals. We used the North American Datum of 1983 for both LORAN-C and DGPS geographic locations.

Evaluating Success of Correcting Position Bias

First, we tested 40 radio-telemetry collars at a DGPS site within Starkey and determined that all collars were functional and provided the same positions. Then two collars were placed approximately 1.5 m above ground at each of 20 random sites within Starkey. A random sample of approximately 300 attempted positions was obtained from each collar, 24-hr each day from 27 October 1992 to 3 November 1992. Each time difference was screened for minimum threshold values of signal strength and signal-to-noise ratios. Two time differences (3-4 time differences in the upgraded automated animal tracking system) that met minimum criteria were used to calculate a UTM coordinate position. The number of usable positions for the analysis varied from 34 to 240 for each collar. For each position, predicted time difference corrections, calculated from block kriging algorithms, was added to or subtracted from each time difference obtained and the corrected position was determined. To evaluate how successfully we corrected bias from our LORAN-C positions we compared UTM coordinates obtained from DGPS at each site with both uncorrected and bias-corrected LORAN-C position estimates for both the original and upgraded automated animal tracking systems. A single measure of error was calculated as the hypotenuse of a right triangle whose legs were the difference between the estimated DGPS and LORAN-C UTM coordinates.

Area Estimates of Radio-telemetry Positions

The same data set that was used to evaluate our success at correcting LORAN-C position bias was used to calculate the area estimates of radio-telemetry positions. Area estimates were based on the distribution of radio-telemetry positions surrounding point estimates at each of the 20 DGPS radio collar sites.

Statistical Analyses

Because bias of LORAN-C positions was spatially autocorrelated, we used geostatistics to interpolate time difference distortions throughout Starkey for LORAN-C transmitters 9940X, 9940Y, 9940W, and 8290Y (Gamma Design Software 1992). We evaluated the degree of autocorrelation among measured data points using semi-variance statistics (Marx and Thompson 1987, Robertson 1987). Isotropic semivariogram models of time difference distortions were obtained with weighted least squares analysis and used to interpolate values for points not measured using block kriging algorithms. We used a jackknife analysis to compare estimated values for each sampled coordinate with actual values.

We used block kriging to estimate time difference distortions for 500 m^2 areas within Starkey for GRI 9940X and 9940Y and 2000 m^2 areas for GRI 9940Y and GRI 8290Y. We estimated time difference distortions for each block with weighted values of 12 nearest measured time differences within a 3,000 m search radius of the block. Points within the block contributed relatively more to time difference distortions than points outside the block.

We used a completely randomized block ANOVA to compare bias of uncorrected data with data corrected for bias (results from block kriging algorithms only) for both the original and upgraded radio-telemetry systems. We used a Student-Newman-Keuls multiple comparison range test to determine whether corrected or uncorrected positions contained less bias.

Results

Magnitude and Extent of LORAN-C Bias

Results from the LORCAL system indicated that biases in LORAN-C positions ranged from 0 to

200 meters in absolute magnitude. The largest biases were found in the northwest corner of the study area.

Success at Eliminating Bias From LORAN-C Radio-telemetry Positions

Summary statistics of isotropic semivariograms for time difference distortions used to evaluate topography-induced bias are presented in Table 1. All correlation coefficients were significant at $P < 0.05$. The results of jackknife analysis indicated that estimates of points were highly correlated for observed time differences ($P < 0.01$).

Position bias varied ($F = 7.79$; 3,57 df; $P = 0.0002$) among groups (Figure 2). We were able to significantly improve accuracy ($P < 0.05$) of the original automated animal tracking system when positions were corrected for bias. The mean difference between corrected and uncorrected positions for the initial automated animal track-

TABLE 1. Summary statistics of semivariograms of LORAN-C time difference distortions measured in μs and used to estimate positioning bias of an automated animal tracking system throughout the Starkey Experimental Forest and Range, northeast Oregon.

LORAN-C transmitter	*n*	Model	Co[a]	Co+C[b]	Ao[c]	r^2	*P*
Middleton (9940X)	372	Linear/sill	0.001	0.021	6650	0.978	<0.0001
George (9940W)	372	Exponential	0.0025	0.0168	839	0.901	<0.0001
Searchlight (9940Y)	14	Exponential	0.00001	0.00711	2840	0.666	<0.05
Williams Lake (8290Y)	14	Spherical	0.000210	0.0452	12600	0.837	<0.05

[a]Nugget variance.
[b]Sill (structural variance plus nugget variance).
[c]Range of autocorrelated data, in meters.

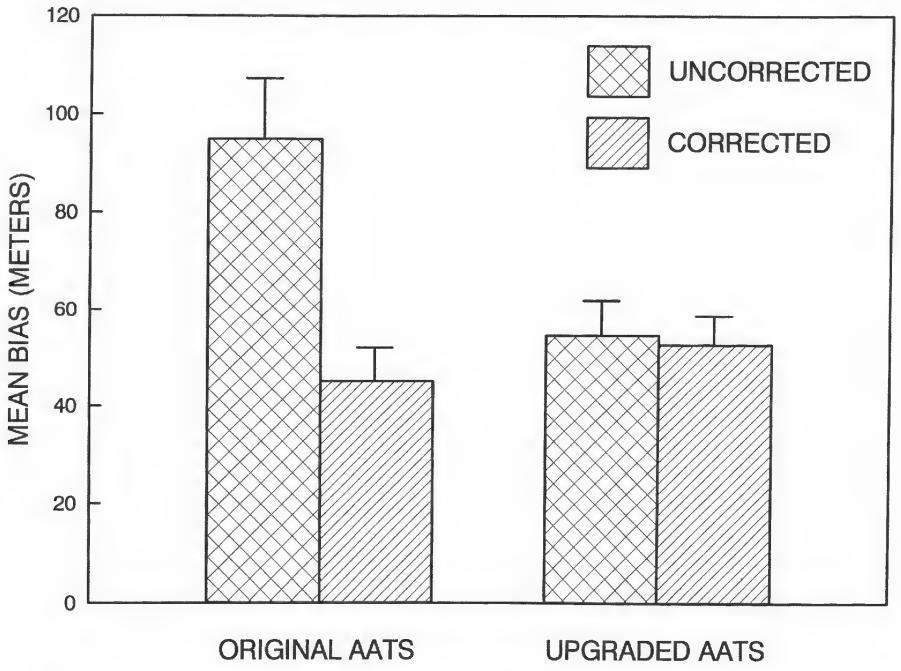

Figure 2. Mean bias and standard error of LORAN-C position estimates ($n = 20$ sites) from the original and upgraded automated animal tracking systems (AATS) used on the Starkey Experimental Forest and Range, northeast Oregon.

ing system was 49.6 m, and at 15 of 20 sites, differences between LORAN-C and DGPS positions were reduced (Figure 2). There was a marked improvement in accuracy of telemetry positions (corrected and uncorrected) in the upgraded automated animal tracking system compared to the original automated animal tracking system because bias was significantly reduced when positions were determined from 3-4 time differences instead of two time differences and because of better configuration of NOCUS chain LORAN-C transmitters in relation to Starkey. Accuracy of positions from the upgraded automated animal tracking system, however, was not significantly improved after corrections were made for bias ($P > 0.05$). Bias was however, reduced at eight of 20 sites.

Mean error of DGPS used at known geodetic reference sites within Starkey was 3.4 m (SE = 0.612, $n = 3$). Using corrections to remove bias from telemetry positions, the area estimate of each position from the original and upgraded automated animal tracking system was 3.4 ha and 3.1 ha (90% C.I.), respectively. The probability that each position is near the center of the area estimate is much greater than near the perimeter.

Discussion

Time- and position-dependent factors influence LORAN-C performance on land. Time-dependent errors, i.e., atmospheric conditions, can be partially removed using differentially-corrected LORAN-C. This technique involves placing a LORAN-C receiver at a base station with a known location. LORAN-C signal variations are measured at the known location and differential corrections are calculated for each remote station time difference measurement. This method is most effective when the distance from base station to remote is small and the terrain is flat.

Differential LORAN-C is less effective for correcting position- dependent biases, especially over rugged terrain (Lachapelle and Townsend 1991). However, proper calibration of a LORAN-C receiver at known positions established with DGPS can be effective at reducing position bias.

We assumed that the source of LORAN-C position biases were mostly the effect of terrain within Starkey. According to Lachapelle and Townsend (1991), the effect of rugged topography on LORAN-C can result in local position biases up to several hundred meters. In addition, these distortions can vary by a few hundred meters per km. Position-dependent bias in LORAN-C can also be caused by power lines and mineral deposits (II Morrow Inc., 1990). Power lines are absent within most Starkey. It seems unlikely that the magnitude of position bias observed at Starkey could have been caused by mineral deposits (Lachapelle and Townsend 1991).

A marked reduction in position bias of final telemetry positions was evident in the upgraded automated animal tracking system compared to the original system. LORAN-C accuracy depends mostly on distance from transmitting stations, the geometry between transmitters, and type of terrain (Boer et al. 1989, White and Garrott 1990). The geometry of the LORAN-C transmitting towers was improved with the addition of two transmitting towers from the NOCUS chain. Also, bias may have been significantly reduced when positions were determined from 3-4 time differences instead of two time differences.

Time difference corrections from geostatistical analysis improved the accuracy of the original automated animal tracking system on Starkey. However, corrections did not remove all the position bias in the original automated animal tracking system. Lachapelle and Townsend (1991) found that LORAN-C biases of 50-100 m represented the limits of accuracy that could be achieved for the calibration of LORAN-C with DGPS. Those researchers also indicated that it was not possible to separate completely the position-dependent conductivity due to ground moisture and terrain effects from the atmospheric and other time-dependent effects. Corrected position bias at Starkey was well within the limits of attainable accuracy of LORAN-C reported by Lachapelle and Townsend (1991).

Corrections from geostatistical analysis for the upgraded automated animal tracking system did not significantly reduce bias. One possibility for the lack of bias reduction is because of our LORAN-C equipment signal-travel-time measuring accuracy (0.1 μs or 30 m), thus reducing our ability to develop more accurate corrections. Also, we measured LORAN-C time differences for 9940Y and 8290Y at 14 DGPS sites which may have been an inadequate sample size given the variability in LORAN-C distortions found with the other two time differences (9940W and 9940X).

We did not pursue reducing bias in the upgraded automated animal tracking system further because it was not significantly different from position bias associated with the original automated animal tracking system after bias corrections were made.

The mean position error of the land-based automated animal tracking system at Starkey of 45.3 m (SE = 7.07) and 52.8 m (SE = 5.87) for the original and upgraded automated animal tracking system, respectively was much better than that reported for other LORAN-C study areas. The mean position error for a stationary, ground based LORAN-C on the Rhode Island coast was 97 m (Patric et al. 1988). Collazo and Epperly (1995) reported a mean position error from 64 to 99 m from a land-based LORAN-C in an estaurine habitat in Core Sound, North Carolina. Leptich et al. (1994) found a mean position error of approximately 200 m for an aircraft-based LORAN-C in northern Idaho.

Radio-telemetry provides a useful technique for studying habitat use and selection by wildlife. However, habitat studies require accurate estimates of an animal's location so that it can be correctly placed in a habitat type (White and Garrott 1986, 1990; Nams 1989). Accurate estimates are especially important when the study area contains a mosaic of small habitat patches because large area estimates may include two or more habitat types. Although both aerial and triangulation radio-telemetry methods often result in errors, these errors are generally ignored when determining environmental characteristics of estimated positions (Saltz 1994). The effect of error in the estimates of positions is to lower the power of tests of habitat selection (White and Garrott 1986).

Mean patch size of the 15 plant community types determined from aerial photo interpretation within Starkey was 14.6 ha (n= 613, SE =4.46; S.L. Findholt, unpubl. data). Size distribution of habitat polygons is skewed toward smaller sizes. Using corrections to remove bias from radio-telemetry positions, the area estimate of the original and upgraded automated animal tracking systems was 3.4 ha and 3.1 ha (90% C.I.), respectively. The accuracy of LORAN-C radio-telemetry positions appears to be adequate for habitat studies being conducted on elk, deer and cattle within Starkey after bias is removed from the position data.

We believe that the methods described in this paper to reduce radio-telemetry position bias can increase the accuracy of LORAN-C collar radio-telemetry; this should result in greater power of statistical tests of habitat selection. In addition, the techniques used to quantify and correct bias from LORAN-C positions at Starkey can also be used to improve the positioning accuracy of non-LORAN-C based radio-telemetry.

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Northwest Science Forum

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Pacific Salmon and the Endangered Species Act[1]

Abstract

There are many ethical, political, and scientific implications surrounding "endangered species," making it difficult to discuss reauthorization of the Endangered Species Act without becoming mired in the pro's and con's of various policy choices. The decline of Pacific salmon is used as a case study to evaluate some of the policy debate surrounding reauthorization of the Endangered Species Act. The challenges posed by listing salmon stocks under terms of the Act are such that everyone in the Pacific Northwest is or will be affected. Viewing Pacific salmon as an endangered species policy issue forces us to evaluate the implications of various policy assumptions. All policy choices involve individual and group winners—and losers—both within and between generations. From a biological perspective, it may be that some stocks of Pacific salmon have been supplanted with fish species better adapted to the current aquatic environment in the Pacific Northwest.

Introduction

There are many ethical, political, and scientific implications surrounding "endangered species," making it difficult to discuss reauthorization of the Endangered Species Act without becoming mired in the pro's and con's of various policy choices. To some the debate over endangered species is simply a matter of choosing among alternatives, much as we do with choices over energy, transportation, or international trade policies. Resolution is merely the process of coming to an agreement by compromise. But others view "endangered species" issues as something akin to religious or moral questions; there is a morally correct position. If one perceives the issue as a moral one, how realistic is it to expect compromise? Still others view "endangered species" through the prism of competing rights—the rights of the public vs. the rights of individuals. An example is "taking" private property without compensation. Another, perhaps hybrid, view is that somehow salmon are linked to our quality of life. It is not primarily a question of the importance of producing trophies for the creel or fillets for the table, but an uneasy feeling that the decline of salmon reflects an intangible loss. It is not surprising that the debate over reauthorizing the Endangered Species Act is characterized by vitriolic attacks on the motives of the combatants.

It is not my intent to advocate a particular position on the salmon issue or for reauthorization or modification of the Endangered Species Act,

[1]Modified from a talk given at the symposium "Reauthorizing the Endangered Species Act: Philosophy, Science, and Politics in Dialog," Oregon State University, Corvallis, Oregon, May 11,1994. The views and opinions expressed do not necessarily represent policy positions of the Environmental Protection Agency or any other organization.

but rather to focus on some of the issues that make reauthorization so controversial, especially as relevant to salmon. If *good* public policy comes from personal and societal experience, and experience comes from *bad* policy, are we at the stage where enough decisions on endangered species have been made that we can now make *good* policy decisions? If so, then one useful way to illustrate the issues is to evaluate case studies in detail to see how the Endangered Species Act actually works—or perhaps doesn't work—as a tool to implement public policy.

There are many interesting candidates from which we can choose. If your fancy leans toward amphibians, we could look at the San Marcos salamander, or something more exotic like the Texas blind salamander; or perhaps the Brunea Hot Springs snail is more to your liking? The California clapper rail or the salt marsh harvest mouse have a certain attraction to some. Or what about an appealing critter such as the Wyoming toad—an unlikely headline grabber in the Rocky Mountains? More emotional and controversial might be the California kangaroo rat, whose habitat requirements mandated under terms of the Endangered Species Act purportedly caused the loss of homes in recent California wildfires.

Salmon

Salmon, specifically the decline of some stocks of Pacific salmon in the Northwest, is my choice. The salmon issue has some complicated factors. No species of North American Pacific salmon is in danger of extinction; however, hundreds of wild stocks (interbreeding, locally defined populations) are at risk. Further, wild stocks in the northern half of the range (northern British Columbia to Alaska) are doing very well, but many in the southern half (southern British Columbia to California) are not. The poor status of wild stocks in the southern half of the range of Pacific salmon is due to a combination of factors, including unfavorable ocean conditions, fishing, dams, water diversions, hatcheries, altered spawning and rearing habitat, predators, and others. Not all stocks are at risk in Washington, Oregon, Idaho, and California, but many are. Alaska stocks and fisheries are booming and salmon aquaculture is thriving in many parts of the world; salmon have never been more abundant in total catch or in the market.

The challenges posed by listing salmon stocks under terms of the Endangered Species Act are such that everyone in the Pacific Northwest is or will be affected. As the saying goes, for the Endangered Species Act at least, salmon is "where the rubber meets the road." On a broad geographic scale, it is in the salmon issue that the goals of species preservation run headlong into many other individual and societal goals (Williams and Williams, 1995; Lackey, 1996a).

Endangered Species Act

Critics have described the Endangered Species Act as "sound-bite policy" based on "barbershop science." In theory, the act takes precedence over all other laws—perhaps even the "takings" clause of the U.S. Constitution (Smith, 1992). Did Congress really understand what it passed? Most of the discussion in Congress concerned the sorry state of bald eagle populations, our national symbol. Were the policy implications comprehended? Were the scientific and technical difficulties considered? How are democratic institutions to choose among the alternatives when the losers lose so big? How do we incorporate the views of those who hold moral or religious views on the propriety of extirpating a species? Is compromise with mutually exclusive alternatives possible? Can public policy be implemented when a "choice" can end up in court for what seems like an eternity? And what is so important about individual species, much less "evolutionarily significant units," whatever those might be? The costs of complying with the Endangered Species Act fall heavily on private landowners who lose land, pay fines, face restriction on use of their property, or watch their investments and business ventures collapse (Gordon and Streeter, 1994). Laws are tools to help implement public policy; what *really* is our policy?

Supporters, on the other hand, maintain that the Endangered Species Act is forcing society to make the necessary, though painful, decisions for the future well-being of society (Rohlf, 1991). And it may not be perfect, but the Act is needed now more than ever, as the decline of Pacific salmon in the southern part of the range illustrates. If changes are needed in the Act, it ought to be expanded to protect ecosystems, not just species. The debate is often framed in moral terms. There may be the token reference to "commodity" value or "surrogate for environmental quality"

but the issue is essentially whether humans have a right to drive a species or other evolutionarily significant unit to extinction (Lackey, 1996b). Other supporters simply point to the economic benefits of commercial and recreational fishing as reason enough to fully implement the Act as written.

If we step back from the immediate challenge of the endangered species/salmon issue, we see that species extinctions are not new in the Pacific Northwest. People have been moving here for the past 15,000 years and causing problems almost from the start. As recently as 10,000 years ago, we still had mastodons, mammoths, giant sloths, giant armadillos, giant beavers, American camels, American horses, the American tiger, and the giant wolf—all are now extinct due to a combination of hunting and naturally occurring climate change. These animals would physically dwarf their surviving cousins. These were *real* animals that would not only survive but prosper in Jurassic Park. However, the size and charisma of a species are not the only measures of importance. Species extinction is nothing new in the Pacific Northwest from the perspective of thousands of years. It is the rate and scale that are the issue these days.

Habitats change due to climatic forces, as well as man's activities, and people develop more efficient ways to hunt, be it by technological breakthrough (e.g., bow and arrow), the use of exotic introductions (e.g., European horse), or by mass marketing of cheap equipment (e.g., monofilament gill net).

More important, the human population of the Pacific Northwest is growing at rates comparable to those in Third World countries. From the successive waves of aboriginal immigration from the North, to the influx of Americans from the East in the past two centuries, to the deluge from the Southwest after the Second World War, the Pacific Northwest has been transformed in a few thousand years from an uninhabited corner of the planet to the most urbanized section of the United States with more than 60% of its population residing in urban/suburban communities. There are other sections of the United States with larger urban populations, but the Northwest is now a region of urbanites—and voters. Like it or not, the human population will continue to grow in the Pacific Northwest and will probably continue becoming even more urbanized. To conclude otherwise is illusional.

Policy

Public choice is choice from among alternatives—the salmon issue is a perfect example. Our choices deal with: How expensive will our energy be? Where will we be able to live? How will we be able to use our private and public property? Which groups will be allowed to fish? Will our food and energy continue to be subsidized? Will we be able to provide jobs for our children? What personal freedoms will we need to give up? It is in the answers to these and other questions that the future of southern stocks will be found. Science can help evaluate the consequences of different alternatives, but the salmon "problem" is fundamentally a *public* choice issue.

But are we chasing a scientific illusion about restoring salmon? The habitat of the Pacific Northwest is dramatically different than it was even a few hundred years ago. For example, the Columbia River basin is now a series of mainstem and tributary lakes. Land use in much of the watershed has changed the aquatic environment in ways that no longer favor salmon. As dramatic as the changes are, some fishes are thriving: walleye, shad, smallmouth bass, and brook trout to name a few. These exotic species are well adapted to the new environment. From an ecological perspective, we may be beyond the stage where we can recreate past salmon habitats. The only option might be to manage for those fishes best suited to current habitat. Another scientifically viable option might be to preserve stocks in those locations such as some "coastal" rivers where the chances of success are greater. Or, as some argue, perhaps we should stop focusing on *stocks* and accept that no *species* of salmon is in danger of extinction. Or is such acceptance merely admitting defeat in the face of difficult and expensive policy choices?

Some offer the promise of adaptive management as the path out of the policy morass. The basic idea underlying adaptive management is that decision makers (and society) learn by experimenting and that decisions get better as we learn through incrementally improving our decisions. The problem is that this approach might work acceptably for problems without moral imperatives and where the alternative decisions are not irrevocable. But, while adaptive management might hold some promise in solving some fairly narrow technical questions, it will not be of much

use in resolving questions of endangered species. Once a species or stock is extirpated, its gene pool is lost forever.

Conclusion

We have been here before: the demise of many Atlantic salmon stocks in the Northeastern United States is the most striking parallel example. Many of those stocks are gone. Atlantic salmon still exist in some locations and the species is in no danger of extinction, but many stocks have disappeared. Genes that survived Pleistocene glaciation were eradicated within a few decades. At least when those policy decisions were made scientists could profess ignorance of genes and gene pools. Now we allocate significant public and private resources in an attempt to restore stocks that are down to a few individuals—stocks that we are attempting to restore to environments not well suited to salmon. When does society say enough is enough? From a scientific perspective, it may be that in some places stocks of Pacific salmon have been supplanted with fish species better adapted to the current aquatic environment. Ocean conditions in the southern half of the salmon's range will undoubtedly improve naturally from a salmon's perspective, but will freshwater and terrestrial conditions? Tough science questions, but tougher policy questions.

Viewing Pacific salmon as an endangered species policy issue forces us to evaluate our policy assumptions. All policy choices involve individual and group winners—and losers—both within and between generations. Unfortunately there are no free lunches. Someone always picks up the tab. So it is with all choices dealing with salmon.

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Book Reviews

Biodiversity and the Law

William J. Snape III (ed.), Island Press, Washington, D.C. ($25.00 paper, $49.00 hardbound)

The conservation of biodiversity is rapidly emerging as a favorite biological mantra trumpeted by scientist-preachers mounting the pulpit at the close of this millennium. While earlier prophets went to the wilderness for revelations about the laws of God, *Biodiversity and the Law* examines the laws of humans for revelations about protection of the full expression of wilderness bioprocesses. If biodiversity protection is accepted as an imperative for human action, this book is an action primer for those looking for ideas and help from the legal system.

The forward to *Biodiversity and the Law* argues that biodiversity is one of those rare ideas that changes the way we think about ourselves. It sets a much higher standard than that of endangered species protection. Human institutions must adapt to accommodate nature and its entire web of interconnectedness. "If you dislike environmental protection, if you thought endangered species protection was faintly hysterical, then biological diversity will send you up the wall." (p. xi) If true, it is easy to explain the paucity of mechanisms for incorporating biodiversity ideas into human institutions. If true, the book is very timely as it examines avenues for law practitioners to institutionalize biodiversity protection.

Those familiar with biodiversity debates realize that the scientific foundation for the discussion has yet to be firmly established in unequivocal terms. One consequence of this is a certain fuzziness in the discussion. The role of scientists will be to increase the knowledge base and precision brought to the conversation about biodiversity. This set of tasks is now underway, but the outcome is still contentious. Many scientists support biodiversity protection, even if it isn't clear what that might mean in practice.

The public acceptance of biodiversity as an important issue is far behind the seminal support of the scientific community. Many "easy sell" pieces of environmental protection gained resonance and support in the public domain. Spectacular national parks, charismatic megafauna, and polluted rivers captured the public consciousness and resulted in support for legislation to protect park lands and endangered species, as well as laws to clean up many aspects of polluted environments. Biodiversity notions will be harder to sell. Ecosystem notions operate at a higher level of abstraction and represent a much greater challenge for future educators hoping to move the public toward support for biodiversity protection.

Biodiversity and the Law operates from the premise that scientists will succeed in establishing biodiversity protection as an important idea, that the public will be educated to call for action to protect biodiversity, and that lawyers will be prime actors in developing protective mechanisms. This book is setting the stage for these developments in the legal profession. It is well constructed to accomplish this task. Although its target audience may be lawyers, it deserves a much wider readership as it is written so as to be accessible to the broader community of readers with environmental policy interests.

The book originated from a conference on biological diversity held in March 1994 under Defenders of Wildlife sponsorship. Sixteen authors combined to produce fourteen chapters that are the meat of the book. Together with an excellent forward, preface, introduction, conclusion and epilogue, the chapters coalesce in a very coherent fashion to tell an important story.

The story is told in four parts. Part I, Biodiversity Law: Where Science and Policy Meet, is a quick study on the nature of biodiversity protection and how it is different from earlier conservation approaches. Although advocates of biodiversity protection are not enemies of earlier approaches (e.g endangered species protection), these approaches are found to be inadequate for the new task of biodiversity conservation. Advocates call for a movement from the focus on conservation problems to a focus on the conservation of processes. Rather than a discussion of particular species, they talk about the importance of theory, ecosystems, scale, and uncertainty. With this as background, even the biodiversity novice

can comprehend the setting for subsequent discussions of protective mechanisms and the law.

Part II, Biodiversity's Safety Net: Saving Endangered Species, deals with the legal history associated with the implementation of the Endangered Species Act (ESA) on both private and public lands. Many policy implications of biodiversity have been tested in the cauldron of ESA experience. Although the protection of endangered species seems like a simple idea, their conservation in practice has been an extremely complex undertaking. Biodiversity conservation will be even more complex. If the law represents the codification of human values, humans had best put a high value on biodiversity because the ESA experience was just a warm up for the battles certain to face biodiversity conservation.

Part III, International Protection: Beyond Human Boundaries, recognizes that no meaningful discussion of biodiversity can stop at national boundaries. If spaceship earth is a metaphor for the global extent of environmental processes, international law is the equivalent metaphor for regulation on a global scale. Although it may be difficult to imagine a world government setting universal legal policy, these chapters deal with the more realistic issues of trade regulation, exotic species, marine environments, and existing international legal instruments as they relate to biodiversity protection.

Part IV, Who Owns What?: A Public Trust for Biodiversity, deals with the assignment of conservation responsibility and "ownership" over the vague, yet intrinsically valuable, biodiversity cache. It argues for an extension of the common law doctrine of the public trust as a starting point for building a new conception of property based on ecological values. Following this, the section delves into currently available legal tools that might be useful in constructing conservation policy to protect ecological values.

The last part of the book considers the prospects of a constitutional amendment guaranteeing citizens a right to protect biological resources. Other nations have set the precedent in their constitutions. By suggesting this for the United States, the legal scholarship exhibited in this book moves biodiversity discussions a long way from the usual discussion of ecologists. Legal scholarship is suggesting an approach to accomplish biodiversity conservation objectives by a change in both law and culture.

In summary, *Biodiversity and the Law* takes the reader into important new directions for consideration in conservation debates. It starts with a short introduction to the scientific and conceptual issues in biodiversity conservation. Building on this knowledge, it explores the challenges facing the legal profession if it expects to protect biodiversity through law and regulation. It ends with a call for a constitutional amendment. This elevates the debate to an arena rarely discussed in scientific circles. The authors have produced an excellent book that deserves a readership far beyond the legal profession.

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Mountain Plants of the Pacific Northwest

by Ronald J. Taylor and George W. Douglas, 1995, Mountain Press Publishing Co. ($20.00)

Recent years have seen the appearance of many new wildflower books and plant field guides, varying in scope and detail, for the Pacific Northwest. This new field guide by Taylor and Douglas covers common vascular plants in the western mountains of Washington, British Columbia and southern Alaska. If for no other reason than its outstanding photographs, this book is definitely deserving of a place on the field botanist's bookshelf.

Authors of a plant field guide have many decisions to make, the answers depending on the intended audience. How many species should be included, and which ones? Which geographical areas should be covered? Which habitats? How should the plants be illustrated with photographs, line drawings, or both? How detailed should the descriptions be, and how technical? Should keys be included? The challenge is to produce a work that is at the same time informative and user-friendly, and thus has appeal for both the expert and the novice. This field guide is for the most part readily accessible to the beginning field botanist. It contains an array of the most commonly seen montane species of the northern Pacific Coast, well illustrated with color photographs. The plants are listed by both common and scientific names (the latter in small print). The descriptions contain little technical language, and technical terms are explained or illustrated at the back of the book.

The book begins with an introduction describing the geographic area and range of habitats covered. The area included in the book is bounded in the south by the Columbia River, in the east by the eastern edges of the Cascade Mountains in Washington and the Coast Mountains in B.C., and in the north by a line running through the St. Elias and Chugach Ranges just north of the 60th Parallel. Habitats cover an elevational range from sea level to alpine, and are divided into several broad zones according to prevailing climate and dominant tree species. It could be argued that northwestern Oregon should also have been included. However, this is clearly a region well known to the authors, both of whom are professional botanists with many years of field experience.

The introductory section is followed by descriptions of approximately 450 plant species, grouped under four headings: ferns and fern-allies, trees (including conifers and hardwoods), forbs and shrubs, and graminoids (grasses, sedges and rushes). Within major groups the arrangement of species is by family. The half-page descriptions for each species include growth form and identifying features of the leaves, flowers, and fruits, along with a brief outline of the plant's ecological characteristics and preferred habitat. The book is arranged throughout with text and corresponding photographs on facing pages, for ease of use. Both growth habit and details of flowers or fruit are shown for many of the plants. Related species are often mentioned, and some of these are illustrated.

The species treated are generally the common ones of this region, with greater emphasis on southern species and those of montane to alpine habitats (the authors are to be commended here for including many of the more distinctive species of grasses and sedges). Most of the common lowland coastal species are included, though less consistently than those of higher elevations; for example, the trout lily or white fawn-lily (*Erythronium oregonum*) and two chocolate lilies (*Fritillaria* spp.) are mentioned, but camas (*Camassia* spp.) are not. Some species of restricted distribution in this area, e.g. western larch (*Larix occidentalis*) and Indian plum (*Oemleria cerasiformis*), are included. However, the book includes all the most commonly seen elements of the native flora.

The final section of the book contains simplified keys to different groups, several pages of line drawings illustrating various plant structures, a glossary, a list of additional useful sources of information on Pacific Northwest plants, and an index. The line drawings are clear and well labeled, and the glossary comprehensive. The index includes both common and scientific names. The authors' professional background is more apparent here than elsewhere in the book, and this section is pitched at a somewhat more advanced level.

A number of criticisms could be made. The scientific names lack authorities throughout, an

omission that may make these names less intimidating to lay users but reduces the book's usefulness for professionals. The common names are not always those most widely used (e.g., fawn lily for *Erythronium montanum*, which lacks the leaf markings from which this name is derived). Some of the pages (especially the introductions to each section) have considerable blank space, which perhaps could have been devoted to additional habitat description or photos, or another species or two. In a somewhat unorthodox arrangement, shrubs are grouped with related herbaceous species rather than with trees, and the lilies and orchids with dicot families rather than with grasses and sedges. I found the keys, especially the key to shrub and forb families, the least satisfactory part of the book. Good botanical keys are not easy to produce, but keys in field guides can be especially problematic because of the difficulty of combining accuracy and comprehensiveness with ease of use. My own preference is to leave the keys to floristic works. For botanists of all levels of experience, leafing through the pictures often works just as well.

Notwithstanding these criticisms, this is a fine book. Its most attractive feature is the excellent collection of photographs, most of them taken by the first author. The illustrations are both beautiful and informative. Many show fine details of the flowers, and for trees, photographs of the bark are also included. Photos are arranged two to four per page, large enough for easy reference. The book is attractively bound, and seems likely to stand up well to use in the field. The text is largely error-free, and the quality of reproduction (both text and illustrations) is high. On the whole, the authors have done well at producing a field guide that will appeal to a wide range of users.

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In a Dark Wood: The Fight over Forests and the Rising Tyranny of Ecology
Alton Chase, 1995, Houghton Mifflin Company, Boston. 535 pages (Cloth, $29.95; ISBN 0-395-60837-6)

Debate over natural resource and ecological policy is often fierce. Whether driving spikes into Douglas fir to discourage harvest or liquidating a company's timber holdings to drive up short term corporate profit and shareholder value, this debate may have more in common with war than democracy. Presidents, governors, business owners, and school teachers can be forced to take sides in debates that offer no safe havens.

Conflict over ecological policy is particularly severe in the Pacific Northwest. The future of forest and range lands, both public and private, is up for grabs. The combatants are engaged in a confrontation of prodigious proportions, a confrontation whose implications few fully appreciate. It is a battle for control of land, but in a larger and more important sense, it is a war of competing cultures, values, and philosophy. The debate is not simply competition between rural and urban residents, between college graduates and high school dropouts, or between workers in the silicon forest and the redwood forest. It is a battle of ideas, a battle of cultures, a battle over the future of western civilization. It is the ideas that interest Alston Chase. Not the protests. Not the Wall Street takeover strategies. Not the policy advocates masquerading as impartial scientists.

The ideas driving the policy conflicts cannot be precisely categorized. On the surface the policy skirmish is over who wins and who loses, but there is a much deeper clash. It is not owls versus jobs, nor is it corporations versus the interests of people. In Chase's view it is a clash between biocentrism ("all living things have equal value") and competing philosophies. The debate over how to define ecosystem management, according to Chase, involves far more than technical aspects; it is fundamentally a debate over the dominant philosophies that underlie western civilization.

This book has at least three goals. The first is to trace the philosophical development of ideas that would eventually spawn the "environmental" philosophy. There really are no good guys or villains here, only the clash of competing philosophies.

The second goal is to explain the current debate over ecological policy issues within the larger philosophical context. Too often, reports on ecological policy debates emphasize the actions of the participants, certainly more appealing to television news producers, but less important than the ideas that precipitate the actions. A confrontation between mill workers and protesters makes great television footage, but what causes such a confrontation?

The third goal is to offer solutions or approaches to resolve some of the conflict. No one seems happy with the current political situation, but what can be done, if anything, to resolve it?

The author's focus is the debate over forests in the Pacific Northwest, primarily the western regions of northern California, Oregon, and Washington. As he tells the story of the forest policy debate, Chase detours to describe the development of a range of divergent ideas, some philosophical, some scientific. A chapter may cover a particularly nasty confrontation between timber workers and environmentalists, but as he quotes ideas espoused by the antagonists, the author will explain how, in his view, those ideas evolved from an earlier time.

Chase adopts the same style to explain some of the science involved in the debates. He will step back and describe how concepts of ecological "health" and "integrity" were developed and marketed in the scientific arena and eventually in the political arena. Even in the scientific arena, he names individuals and often speculates on their political motives.

Phrases such as "Equal rights for all species," "Loggers are people too," "Back to the Pleistocene," and "Environmental fascism " are not merely slogans to Chase, they represent religious and moral positions. From the perspective of academia and government, or from outside the region, such slogans may be dismissed along with the latest campus protest or "wise use" hyperbole. Should they be? Not according to Alston Chase.

He also follows the evolution of the free market philosophy, describing in detail its emphasis on individual autonomy. In contrast, he traces some

of the roots of environmentalism to the area of progressive unionism and the idea of community good. Chase's background as a philosophy professor is apparent in his writing.

The role of government and the bureaucracy is covered in detail, especially as it relates to the Pacific Northwest forest issue. For example, the author detours to describe how the government employees who drafted versions of the Endangered Species Act hid, intentionally or not, the ramifications of the legislation from Congress; members of Congress thought that the Endangered Species Act would deal with, at most, a few hundred species. As interesting as these detours are, they sometimes break up the chronological flow of the book.

Chase describes how the people in timber towns across the Pacific Northwest were caught between competing paradigms of which they understood little. Even after the political die had been cast that sealed their fate, they never really understood the motivation of their opponents. It is this group that garners Chase's sympathy. Held in disdain are the scientists who have stepped from the scientific "is" to the advocacy "ought;" scientists—ecologists in particular—who have used science to argue in favor of biocentric policy positions. Chase contends that science may be used to describe what *is* the condition or characteristic of an ecosystem or to predict the ecological consequences of various decision options, but science cannot be used to render judgement of what option *should* or *ought* to be adopted.

Chase is generally successful in meeting the goals he has set. He tackles issues that are difficult and emotionally charged. He pulls no punches and is particularly hard on scientists who operate as policy advocates. In fact, many readers will feel challenged by his confrontational writing style. To his credit he does not attempt to settle debates with platitudes, an all too frequent cop-out for authors addressing ecological policy.

Some "pop ecology" ideas are attacked with apparent glee. Chase is blunt in shattering the myths of a pre-1492 "pristine" North America, the "balance of nature," and concepts of ecological "health." Such information may not surprise scientists, but his manner of presentation will likely infuriate environmentalists who often prefer the myth of a pre-European pristine landscape. He makes short work of the desirability of managing ecosystems to "presettlement" conditions. None of this is new to scientists working on ecosystem management issues, but Chase's brusqueness may offend some readers. Readers with environmentalist political leanings should expect to be challenged.

I found myself squirming as he portrayed many ecologists as little more than handmaidens for environmentalists. Perhaps because this is closer to home, I am more sensitive. His condemnation is not categorical, but his tone is dismissive. Ecologists who use their scientific background and positions, especially taxpayer paid, to argue for political (generally environmentalist) positions warrant scorn, according to Chase. He argues that many, perhaps most, ecologists have lost their credibility as scientists because they have become spin doctors for environmentalist positions.

Clarifying the proper role of scientists, particularly ecologists, in formulating public policy is important. Some categorize ecologists as pseudoscientists, little more than "environmentalists" who use their scientific credentials to lobby for particular public policy positions. Others regard ecologists as analogs to physicians, technical experts who can help explain to decision makers and the public the consequences of policy alternatives without advocating any particular position. In Chase's mind, there is no doubt where most of us would be categorized.

Much of what is written today about biological diversity, ecosystem stability, ecosystem health, and sustainability accepts as a premise a biocentric world view. Whether or not one agrees with the biocentric position in the philosophical debate, it is this premise (or the alternatives) that largely defines debates; consequently this issue deserves a larger portion of the public discourse.

Chase is a good writer and his book is worth reading. Whether you agree or not with his interpretations of ideas and events, he presents information in an interesting, provocative manner. Because he is so direct, he is likely to offend those with strongly held environmentalist positions.

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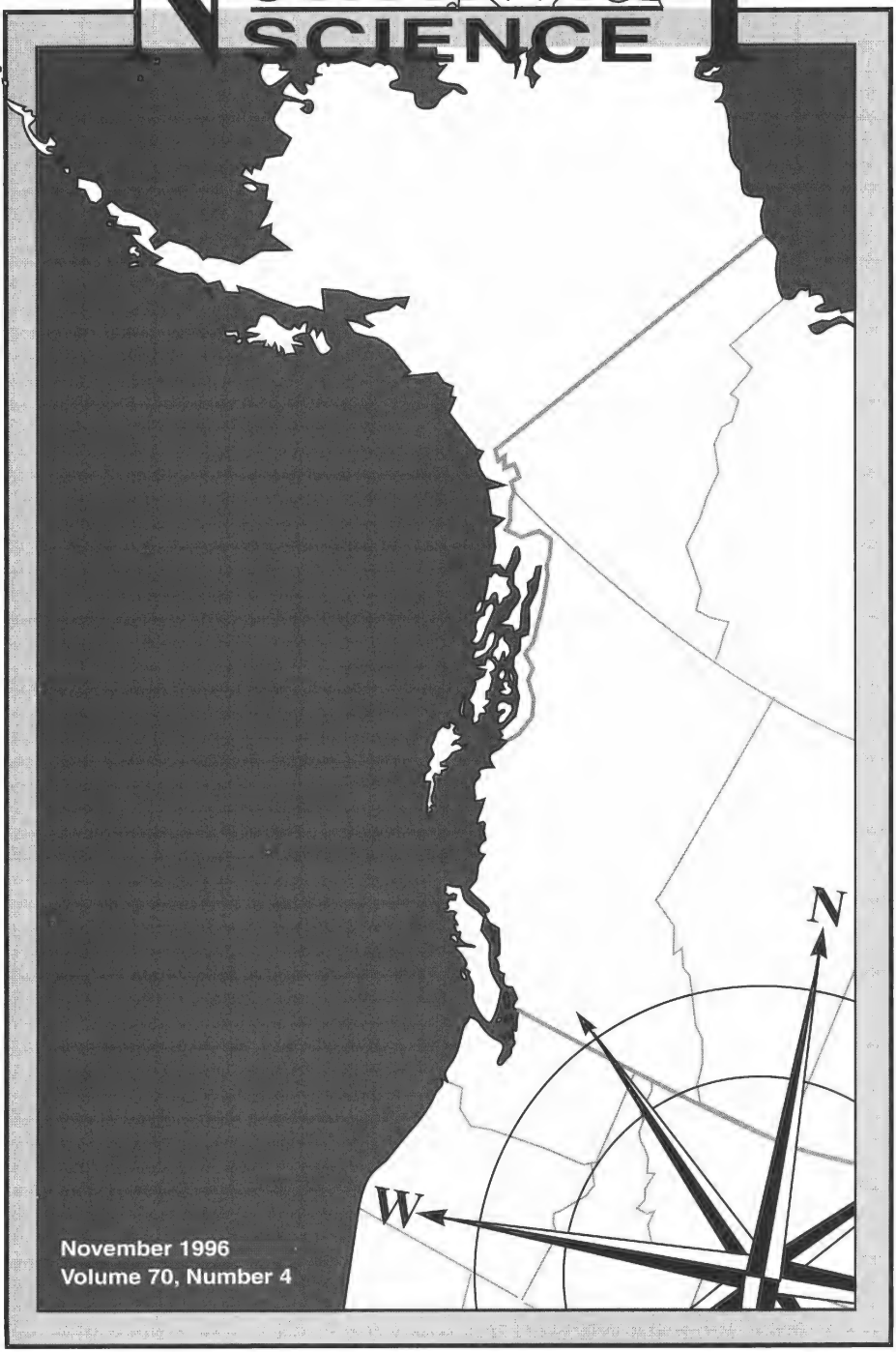

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Announcements

1997 Annual Meeting

The 70th annual meeting of the Northwest Scientific Association will be hosted by Eastern Washington University and held at the new Riverpoint Campus in Spokane, Washington. The meetings will be held jointly with the Lichen Guild and the Society for Experimental Biology and Medicine on March 26-28, 1997. Following a business meeting for the Board of Trustees on March 26, scientific sessions will occur on the following two days with a variety of concurrent sections and symposia. Work is currently underway for symposia on Northwest aquatic systems, archaeological studies in the Northwest, and Inland Northwest biotechnology. Field trips will focus on the Columbia Plateau and natural areas of northeast Washington and adjacent Idaho.

Both members and nonmembers of the Northwest Scientific Association are welcome at the meetings, and students are especially encouraged to attend.

Visit our Web Page!

Information about the Northwest Scientific Association and on all aspects of the 70th annual meeting (including accommodations and section and symposium topics) will be available and constantly updated on our World Wide Web site. The address is:

http://www.csmt.ewu.edu/csmt/nwsci/nwsci.htm

Postcard Promotional

In the interior of this issue is a postcard, enabling members to promote *Northwest Science* among peers, students, and potentially interested organizations. The involvement of each member is vital for enlisting new members in NSA. Samples of the journal will be sent to designated recipients. Take advantage of this convenient opportunity to spread the word about *Northwest Science*!

1997 Student Research Grants

Student Research Grants are provided by the Northwest Scientific Association to help students complete scientific research projects. Funding should be used only to support research activities of the student. It is expected that students will report their research results at a future NSA meeting.

Eligibility—Applicants must be regular members of the Northwest Scientific Association.

Preparation of the Proposal—A cover page should include: (1) name and address of applicant, (2) associated institution, (3) name of major professor/advisor, (4) degree program, (5) year in school, (6) amount of funding requested (maximum of $500 [US]).

The proposal should include: (1) title, (2) statement of justification, (3) methodology/study design (including analytical methods), (4) detailed budget. The proposal should be no more than three typed, double-spaced pages (excluding cover page and budget).

Proposals are due on or before 7 February 1997, and should be sent to: Dr. Jerry O. Wolff, U.S. Environmental Protection Agency, 200 SW 35th Street, Corvallis, Oregon 97333 (tel.: 541-754-4377, fax: 541-754-4338, email: jerryw@mail.cor.epa.gov). Grants will be awarded at the 1997 annual meeting of NSA.

Announcements, continued next page

Should *Northwest Science* Go Electronic?

An increasing number of scientific journals are being published in electronic format. This can increase the efficiency of the review and publication process, as well as save printing and distribution costs. Should *Northwest Science* be published in electronic format at some point in the future? What would be the potential positive and negative outcomes of this transition? This topic will be discussed at future meetings of the Northwest Scientific Association Board of Trustees and with Washington State University Press, our publisher. Please send your opinions on this topic to the Editor, preferably via e-mail at wild@u.washington.edu.

Seventy Years of *Northwest Science*—Charting Our Future

Readers should pay special attention to the Forum section in this issue of *Northwest Science.* An article by Sono Hashisaki discusses the use of restoration techniques in wetlands. Restoration ecology is a relatively new area of science, and the integrative approach used in this paper is an increasingly common approach found in the pages of *Northwest Science* and other journals.

Another Forum submission by R. Gerald Wright discusses trends in the scientific emphasis of all 1634 papers published in the 70-year history of *Northwest Science.* We are grateful to Dr. Wright for this ambitious summary and would like to highlight a couple of points from his article. While we have always welcomed papers from all scientific disciplines, the analysis shows a strong trend in recent years toward a predominance of papers in the natural sciences. Although our editorial board is capable of reviewing papers in nearly any field, we have very few submissions in social science, physics, chemistry, and educational aspects of science. These topics are rarely addressed in sessions at the annual meetings of the Northwest Scientific Association.

Based on his analysis, Dr. Wright suggests that *Northwest Science* and NSA should consider an exclusive focus on the biological/ecological sciences in order to enhance the value of the journal and strengthen NSA. As he points out, there is considerable multidisciplinary breadth in the natural sciences alone. **What do readers and NSA members think? Is it time for a change? Your opinions are needed to address this issue.** Please send comments to the Editor (preferably by e-mail: wild@u.washington.edu), and they will be distributed to the NSA officers and Board of Trustees. You are also invited to send a letter or article for the Forum. Thanks for your input.

—The Editor

Notice of Proposed Changes in theTerm of President and Resulting Constitutional Changes.

At the October business meeting in Ellensburg, the Governing Board voted to change the term of President of Northwest Scientific Association. The proposed change increases the term of President to two years, preceded by a one-year term as President Elect and followed by a one-year term as Past President. The decision was based on a perceived need to increase the continuity and therefore the effectiveness of the office. Additionally, it was felt that this would remove from the President many of the current activities related to the annual meetings and allow the individual to play a greater role in leadership as regards the Governing Board.

A change such as this involves a constitutional change which requires a vote of the membership. As current President of the NSA, I will call for two votes on this matter at the business meeting in March of 1997. One vote will be for acceptance or rejection of the proposed change in presidential term and the other (if the first is passed in the affirmative) will be for ratification of the proposed constitutional change (as follows).

Please give this some thought and come prepared to discuss the issue during the March meetings.

—R. L. Carr, President

Announcements, continued next page

The proposed change in the wording of the Northwest Scientific Association constitution follows. Wording that is to be added is underlined. Wording that is to be removed is shown in brackets [ ].

Article IV. Officers

The officers shall consist of a President, President Elect or Past President, Secretary and Treasurer.

[All officers] The President Elect, Secretary and Treasurer shall be nominated by the nominating committee or by members from the floor at the annual meeting ; the President Elect and President shall automatically advance to the office of President and Past President, respectively, at the conclusion of their term of office.

Election shall be by vote of members present at the annual business meeting and those elected shall assume their office at the conclusion of the meeting.

To enhance continuity, all officers shall normally be elected from the membership of the present or recent past Governing Boards.

The program chairman may be appointed for a one year term by the president and shall normally be from the campus which hosts the annual meeting.

Vacancy of the office of President is filled by advancement of the President Elect , if there is an incumbent President Elect; in the absence of a President Elect, the vacancy shall be filled by vote of the Governing Board. Replacements for vacancies in other offices shall be appointed by the President.

The term of the President shall be two years, beginning with the annual meeting in even numbered years.

The term of the Past President and President Elect shall be one year , beginning with the annual meeting in even and odd numbered years, respectively.

The term of the Secretary or Treasurer shall be three years.

Article VI. Governing Board

Section 1. The Governing Board of the Association shall consist of [Twenty-two] twenty-one members. The officers of the association, the editor of Northwest Science, and the Program Chairman[, and the immediate past President] shall serve ex-officio (with vote). The remaining fifteen members (Trustees) shall serve 3 year terms. Five trustees shall be elected each year to replace those whose terms expire.

Vacancies, including those arising from the election of a Trustee to one of the ex-officio offices, shall be filled by the president as they occur. The person so appointed shall hold office until the next regular election at which time a member shall be elected to fill the remainder of the unexpired term.

Jeffrey C. Lewis[1] and **William J. Zielinski,** USDA Forest Service, Pacific Southwest Research Station, 1700 Bayview Dr., Arcata, California 95521

Historical Harvest and Incidental Capture of Fishers in California

Abstract

Recent petitions to list the fisher (*Martes pennanti*) under the Endangered Species Act have brought attention to fisher conservation. Although commercial trapping of fishers in California ended in 1946, summarizing the commercial harvest data can provide a historical perspective to fisher conservation and may indicate the prevalence of incidental fisher captures in traps set for other species. We investigated the relationships between historical fisher harvests and the price paid for fisher pelts, number of trapping licenses sold, cost of a trapping license, total number of 5 sympatric species harvested, and their pelt prices in California. The frequency of incidental captures was also assessed by interviewing trappers, biologists, and wardens in California. Between 1919-1946, relatively few fishers were legally trapped in California ($n = 462$, $\bar{x} = 18.5$ annually), and their harvest declined steadily. Fisher harvests were positively related to fisher pelt price but were more strongly related to the number of trapping licenses sold, indicating that fishers were vulnerable to trappers in general as opposed to only those trappers specifically targeting them. We estimated an incidental capture rate of 1 per 407 set-nights and a mortality-injury rate of 24% from data obtained from 5 trappers in California. Trappers are an important source of information on the distribution of fishers and their cooperation is necessary to determine the effects of incidental capture on fisher populations.

Introduction

Fishers (*Martes pennanti*) were legally trapped in California until the season was closed in 1946. The number of fishers harvested in California from 1919 to 1946 declined steadily (Seymour 1980) and several authorities voiced concern that trapping was threatening populations of fishers, martens (*Martes americana*) and wolverines (*Gulo gulo*) (Dixon 1925, Grinnell et al. 1937, Hall 1942). It was asserted that fishers were captured predominantly by a small number of trappers and hunters specifically seeking, and proficient at capturing, fishers (i.e., fisher specialists; see Grinnell et al. 1937:229). Specialists were held largely responsible for the decline in the fisher population reflected in the harvest. While fishers were legally trapped in California, their pelts were the most valuable among furbearers (highest mean price per pelt; Calif. Dept. of Fish and Game, Sacramento, unpubl. data), thus rewarding their specific pursuit. Nonetheless, the capture of fishers by trappers seeking other furbearers was not uncommon (e.g., Hamilton and Cook 1955, Benson 1959, Coulter 1960, Balser and Longley 1966, Weckworth and Wright 1968, Yocum and McCollum 1973, Cottrell 1978, Pack and Cromer 1981, Strickland and Douglas 1984, Aubry and Houston 1992, Marshall 1992, Cole and Proulx 1994), and it is likely that incidental captures contributed to the legal harvest of fishers in California. In fact, when the closure of the fisher season was being considered in California, Hall (1942) related (but did not agree with) the common opinion at the time that closing the season would have little effect because fishers were so frequently taken in sets for other species.

In the 1994-1995 season, 313 trapping licenses were sold in California; many of which were used to pursue terrestrial carnivore species that often are sympatric with fishers. Although fishers cannot be legally targeted in California, they are considered one of the easiest animals to capture (Coulter 1960, Young 1975, Powell 1993). But, because they are not legal quarry their capture and condition at release are rarely reported. Moreover, fishers frequently receive serious injuries in leg-hold traps (Cole and Proulx 1994) and even low rates of additive mortality from trapping have been predicted to affect fisher population stability (Powell 1979). Fisher conservation may be hindered by the lack of information on the amount and effects of incidental capture.

Fishers are absent from significant portions of their range in California (Zielinski et al. 1995) and the western U. S. (Gibilisco 1994, Powell and Zielinski 1994), and have twice been petitioned for listing under the Endangered Species Act in the western U. S. (Central Sierra Audubon Society 1990, Biodiversity Legal Foundation

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1994). It is currently listed as a Species of Special Concern by the State of California.

Here we summarize the historical fisher harvest data in California to attempt to understand the relative rates and importance of incidental harvest of fishers by generalist trappers versus captures by fisher specialists. We examine the effects of the price paid for pelts (for fishers and other sympatric furbearing species), number of licenses sold, and cost of a license on the number of fishers harvested. We also estimate the current rate of incidental capture by conducting interviews with trappers and summarizing recent data from the literature.

Methods

We defined incidental captures as those captures that occur in sets made specifically for species other than fishers; illegal captures were not included among incidental captures. Generalist trappers were defined as those who were not specifically seeking fishers, but who may have captured them incidentally while targeting other furbearers.

Historical Fisher Harvest

Data on annual harvest, pelt price, and licenses (number sold and purchase price) were obtained from California Department of Fish and Game (CDFG) and Grinnell et al. (1937) for commercial trapping seasons between 1919 and 1946 in California, excluding data from the 1928-1929 and 1929-1930 seasons which were unavailable; resulting in 25 years of fisher harvest data. The cost of a trapping license was $1.00 from 1917 to 1946. A consumer price index (U. S. Department of Labor, Bureau of Labor Statistics) was used to adjust the price of pelts and licenses for inflation to a 1982-1984 baseline. Analyses were conducted using adjusted license and pelt prices only.

We assessed relationships between the number of fishers harvested and the price of fisher pelts, number of licenses sold, number of sympatric species harvested, and the price of sympatric species' pelts using linear and multiple regression. Limited data precluded the use of extensive multiple regressions (Johnson 1981). Sympatric species included coyotes (*Canis latrans*), bobcats (*Felis rufus*), raccoons (*Procyon lotor*), gray foxes (*Urocyon cinereoargenteus*), and ringtails (*Bassariscus astutus*), collectively referred to as CBRGRs. CBRGRs are considered sympatric with fishers where fishers occur, but they also occur in areas of California outside of the range of the fisher (Ingles 1965). CBRGRs were probably the most sought after terrestrial furbearers because of their pelt prices and relative abundances. The total number of sympatric species harvested was combined annually. The mean prices of pelts for each sympatric species were averaged to create a grand mean price of pelts of CBRGRs. We also assessed the relationships between annual sales of licenses, the price of licenses, and the price of pelts of CBRGRs; and between the number of CBRGRs harvested, the number of licenses sold, and the price of pelts of CBRGRs. Due to their ease of capture we suspected that both the commercial (when fisher trapping was legal) and incidental (past and present) capture of fishers would increase with effort expended toward the capture of CBRGRs (the generalist contribution to the number of fishers captured). Analyses were limited because data for the number of fishers harvested and the number of licenses sold were available only for the State as a whole, not for individual counties or regions, and records of take by individual trappers were unavailable.

Incidental Capture of Fishers

Selected California trappers, and CDFG wardens and biologists were interviewed to estimate the rate of incidental capture of fishers. Five trappers were interviewed about their trapping effort, and the number and condition of fishers captured. "Set-nights" were used as a measure of effort and equaled the number of sets (specific locations where usually 1 or 2 traps were set) multiplied by the number of nights when traps were set. The number of incidental captures of fishers was then divided by the number of set-nights to estimate the incidental capture rate. We also reviewed literature on fisher management to characterize the frequency and relative importance of incidental captures of fishers by commercial trappers in the U. S. and Canada.

Results

Historical Harvest Analysis

Number of Fishers Harvested and Price Paid for Pelts. A total of 462 fishers were harvested in California from 1919 to 1946 (annual $\bar{x}$ = 18.5,

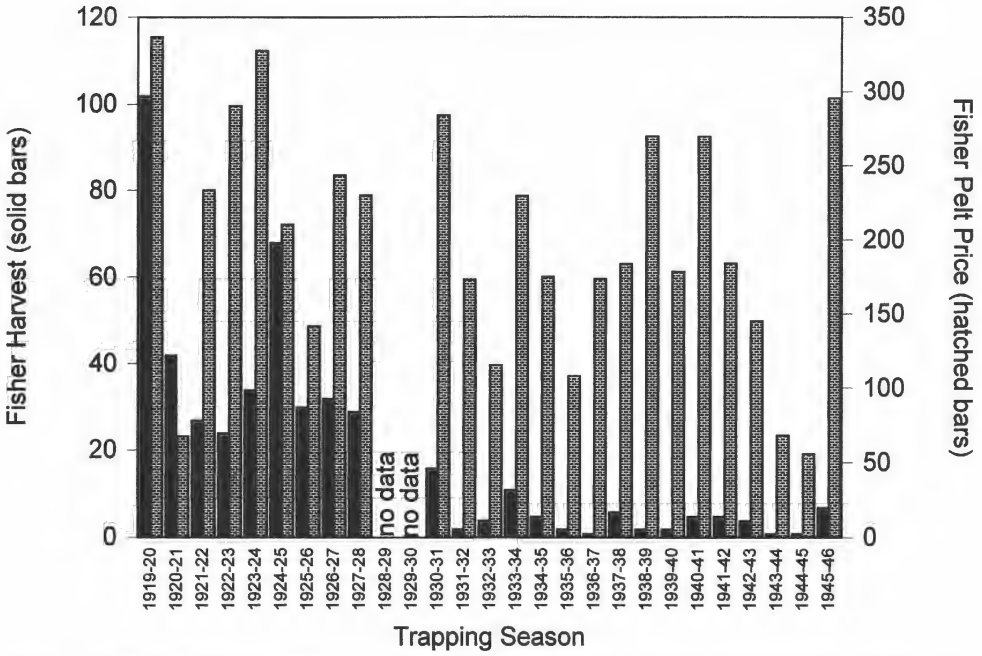

Figure 1. Number of fisher pelts harvested and the mean price paid (adjusted for inflation) for fisher pelts in California, 1919-1946.

SE = 4.8, range = 1-102). Harvest declined steadily, but pelt price varied considerably during this period (Figure 1). The number of fishers harvested was related to the price paid for fisher pelts (r^2 = 0.16, P = 0.049).

Number of Fishers Harvested and Number of Licenses Sold. The number of fishers harvested was most strongly related to the number of licenses sold (r^2 = 0.50, $P < 0.001$). In a multiple regression analysis, the number of fishers harvested was significantly related to the number of licenses sold (F = 4.12, $P < 0.001$) but was unrelated to the price paid for fisher pelts (F = 1.05, P = 0.303). The number of licenses sold was most strongly related to the mean price paid for CBRGR pelts (r^2 = 0.39, $P < 0.001$) and was negatively related to the cost of a license (r^2 = 0.21, P = 0.021). When adjusted for inflation, the price of a license ranged from $5.00 to $7.69 during the period when fisher trapping was legal.

Number of Fishers Harvested, Number of CBRGRs Harvested and Price Paid for CBRGR Pelts. The number of fishers harvested was positively related to the price paid for CBRGR pelts (r^2 = 0.29, P = 0.005), but not to the number of CBRGRs harvested (r^2 = 0.07, P = 0.197). The number of CBRGRs harvested was most strongly related to the price paid for CBRGR pelts (r^2 = 0.25, $P < 0.001$) and to the number of licenses sold (r^2 = 0.36, P = 0.002).

Incidental Capture of Fishers

Interviews with California trappers indicated that they captured fishers while trapping for bobcats, gray foxes, coyotes, and raccoons. Interviewed trappers reported 72 incidental fisher captures over 50,908 set-nights (Table 1). The incidence of injury or mortality was as high as 75% (Table 1). Several trappers, and CDFG biologists and wardens provided information concerning fisher poaching, and the illegal sale of fisher pelts out of state.

Discussion

The decline in the number of fishers harvested from 1919 to 1946 in California has been attributed to overharvesting by fisher specialists (Dixon

TABLE 1. Set nights and incidental fisher captures of trappers from Northern California[a].

Trapper	Set-nights	Time Period	Captures (set-nights/ capture)	Mortalities and injuries	Mortality and injury rate[b]
1	41,600	13 seasons	7 (5943)	1	0.143
2	5,000	4 seasons	20 (250)	15	0.750
3	2,700	2 seasons	27 (100)	1	0.037
4	600	1 season	16 (38)	0	0.000
5	1,008	1 season	2 (504)	0	0.000
Total	50,908	21 seasons	72 (407)	17	0.236

[a] Trapping occurred in Trinity, Shasta, Humboldt, and Mendocino Counties.
[b] Number injured and dead/number incidentally captured.

1925, Grinnell et al. 1937, Hall 1942). The susceptibility of fishers to incidental capture, however, suggests that fisher populations are also vulnerable to trappers seeking other furbearers. Although the number of fishers harvested and the price paid for their pelts were related, the number of licenses sold, not pelt price, explained a significant amount of variation when the pelt price and annual license sales were included in the same multiple regression model. While this conclusion differs from the relationship between fisher pelt price and number of fishers harvested in Canada from the period 1948-1977 (Powell 1993), it is consistent with the lack of relationship between pelt price and number harvested in Canada for the period 1920-1942 (Rand 1944).

For many furbearing species the number of pelts that are harvested frequently correlates positively with the market price of the pelt (e.g., Erickson 1980, Obbard et al. 1987). However, generalist trappers seek to maximize the opportunity of capturing any of the commercial species and their efforts, reflected by the number of licenses sold and mean price of pelts of CBRGRs, can also affect the capture of fishers. If the number of licenses sold measures overall trapping effort for terrestrial carnivores, it would appear that the number of legally trapped fishers in California was affected more by generalist trapping effort than by the price paid for fisher pelts. Consequently the decline in the number of fishers harvested during the period 1919-1946 reflects either a decline in the number of fishers or the decline in the number of licensed trappers (CDFG, unpubl. *data*). *Overtrapping by specialists* (Grinnell et al. 1937) may have played some role in the decline but our analysis suggests that harvest by trappers who were not specifically seeking fishers was another important factor.

The number of licenses sold serves as an index of effort to capture terrestrial furbearers and therefore reflects the opportunity to capture fishers. Why then was the number of fishers harvested not significantly related to the number of CBRGRs harvested, but only to the number of licenses sold and the price paid for CBRGR pelts? This is best explained by dividing the fisher harvest into 2 parts: the portion taken by fisher specialists who were motivated by fisher pelt price, and the portion taken incidentally by generalist trappers who were motivated to capture CBRGRs. A proportionately larger harvest by fisher specialists would be expected to result in a strong relationship between fisher pelt price and fisher harvest, however we found a weak relationship at best. A proportionately larger harvest by generalist trappers would be expected to result in a strong relationship between CBRGR harvest and fisher harvest, but this was not observed. Therefore, the total harvest probably consists of a balance between the specialist and incidental portions. Consequently, the number of trappers (both generalists and specialists), as reflected in the number of licenses sold, best explains the number of fishers harvested.

The threat of incidental capture has been an important consideration in the management of fishers in the Pacific States and elsewhere. Oregon prohibited trapping in large areas surrounding fisher reintroduction sites to avoid accidental capture (Kebbe 1961, Berg 1982; see also Marshall 1992), and in Washington, incidentally trapped animals accounted for much of the historical and recent information on its distribution (Dalquest 1948, Aubry and Houston 1992). A recent decline

in the fisher population in British Columbia precipitated the closure of the fisher season in 1991-92, but trappers were allowed to retain 2 fishers in the 1991-92 trapping season because incidental captures were considered unavoidable (British Columbia Ministry of the Environment, Lands, and Parks, unpubl. data). A recent plan to assess the effects of forest practices on species associated with old-growth in the Pacific Northwest (Thomas et al. 1993) suggested that restricting marten trapping in areas where fishers were suspected to occur would mitigate the effects of habitat loss on the latter by reducing mortality from incidental capture.

The consequences of incidental capture of fishers have also been documented outside the Pacific States and British Columbia. Using data collected during a year when the fisher season was closed in New York, Parsons (1980) estimated that incidental fisher captures amounted to 30% of the annual harvest when the fisher season was open. Data from New York and Maine strongly suggested that most trappers caught fishers while seeking bobcats, foxes, beavers (*Castor canadensis*), or coyotes (Hamilton and Cook 1955, Coulter 1960, 1966). Clark (1986) stated that in Maine "fisher are captured in all types of land traps; therefore any individual who sets a land trap can be classified as a potential fisher trapper." In Minnesota and Wisconsin, the recovery of protected populations of fishers was indicated by the increasing number of animals accidentally captured in traps set for other species (Irvine et al. 1964, Balser and Longley 1966). In New Brunswick, a short open season was authorized in 1963 because trappers complained that they "could not keep fishers and martens out of their traps" (Dilworth 1974). Over a 9 year period following the fisher reintroductions in Nova Scotia, 32 fishers were accidentally trapped in sets for other animals (Dodds and Martell 1971). During a 5-year period when fishers were protected in Idaho, Luque (1983) estimated that at least 163 were inadvertently trapped in sets for coyotes, bobcats, and martens. And, in the 6 years following a reintroduction of fishers in Montana, 7 were submitted to authorities after being taken in traps set for mink (*Mustela vison*), wolverines, bobcats, and lynx (*Lynx lynx*) (Weckwerth and Wright 1968). Incidental captures reported among studies may be only a fraction of the number of fishers actually taken, as trappers may be reluctant to report the capture and condition of a protected animal.

If fishers that are unintentionally captured were always released unharmed the frequency of incidental captures would be of little concern. However, as evidenced by our sample of California trappers (Table 1), this is not always the case. It is unlikely that a trapper can assess the extent of an animal's injuries in the process of releasing it from a trap, especially internal injuries. Therefore we consider the reported mortality/injury rates (Table 1) as minimum estimates. Captured fishers are recovered dead in traps, are killed by other animals while trapbound, and will injure themselves in an effort to escape (Strickland and Douglas 1984). Fourteen of the 163 fishers estimated to be incidentally captured in Idaho were dead in traps, but many more were probably discarded (Luque 1983). Coulter (1966) reported that in 1950, 23 (of 139) fishers captured were lost when they "broke legs in the traps and escaped" and that the ratio of injured animals was about 1 out of 5. In a recent review Cole and Proulx (1994) found that 18.5% of 762 fishers trapped with leg-hold traps had trap-related injuries (broken bones, swelling and hemorrhage, or self-mutilation). In addition, fishers are considered formidable when trapbound and struggle persistently (Coulter 1960), and injuries or death can result from poorly managed or unsuccessful releases. One of the trappers we interviewed caught 20 fishers and was able to release 5 of these unharmed; 14 of the other 15 were injured and another was killed by coyotes. This trapper explained that fishers were difficult to release and that the injuries he observed may have resulted from his use of larger traps (sizes 2 and 3). The subsequent survival of incidentally captured and released fishers (assumed to be 50% by Douglas and Strickland 1987) may negatively affect existing populations or prevent the recovery or establishment of others. Powell (1979) predicted that the removal of as few as one to four fishers per 100 km^2 via trapping would result in a decline of a midwest population. The magnitude of the effect of additive mortality would depend on the sex and age of the captured individuals (Krohn et al. 1994), and may be greater in western populations since they have not demonstrated the rapid population recovery after protection that has been observed in eastern populations (Powell and Zielinski 1994).

The number of trapping licenses sold today in California is relatively small by historical standards and trapping licenses are not inexpensive ($64.25 in 1995-1996). Thus, at first glance it might seem that the effect of trapping on a rare carnivore, like the fisher, would be relatively minor. Moreover, because the use of padded leg-hold traps was implemented recently in California, injuries to non-target species are probably fewer. Although the population of trappers may be on the decline and traps are less likely to injure captured animals, the potential effects of legal trapping of other species on protected fisher populations should not be ignored, especially when considered in conjunction with habitat loss (Powell and Zielinski 1994) and other sources of mortality (e.g., roadkills). The increased number of licenses sold in the late 1970's and early 1980's in response to higher fur prices (>3000 licenses sold from 1979-1983; CDFG, unpubl. data) may have increased incidental fisher captures in the recent past. As compared to when fishers were legally harvested, trappers now have greater access to remote areas (see Hodgman et al. 1994) and they can trap much larger areas. Although traps are required to be checked daily in California, the number of traps that can be run by an individual is unlimited. Further, we have no idea how many incidental captures are too few to affect populations.

Given that incidental capture was a component of the historical commercial harvest and still occurs today, CDFG should seek trapper cooperation in monitoring incidental take. Trapping regulations should require the reporting of (and providing specific information about) incidental captures of fishers and other protected carnivores, and trappers should be compensated for this information. For example, photographic documentation of a capture could be required to receive a nominal reward. Alternatively, wardens and biologists could randomly accompany trappers as they check their lines. This could also apply to the capture of other uncommon and rare forest carnivores including martens, wolverines, and Sierra Nevada red foxes (*Vulpes vulpes necator*). Incidental capture reports should include the date, location of capture, estimated sex and age, verified identity (via photograph), and condition upon release. This information will contribute to a growing database of location information to describe present distributions of rare carnivores. Considered alone, the 72 records of fisher captures by the small sample of trappers we interviewed would make a significant contribution to our knowledge of fisher distribution in California. A reliable index of incidental capture would also make it possible for managers and researchers to determine the effects of incidental captures on populations of fishers and other uncommon forest carnivores.

Acknowledgements

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Diet of Yearling Chinook Salmon and Feeding Success During Downstream Migration in the Snake and Columbia Rivers

Abstract

The objectives of this study were to characterize and compare the stomach contents and feeding success of yearling chinook salmon smolts (*Oncorhynchus tshawytscha*) during their downstream migration at three sites in the Snake and Columbia Rivers. From 1987 to 1991, 26 to 38% of the yearling chinook salmon smolts sampled as they passed Lower Granite Dam, the first dam encountered by migrants in the Snake River, had empty stomachs. In 1991, smolts were sampled further downstream at McNary and Bonneville Dams on the Columbia River on the same sample dates. Empty stomachs occurred in 3% and 5% of these fish, respectively, and overall stomach fullness values were significantly higher. Smolts ate primarily dipterans (chironomids) at Lower Granite Dam; cladocerans, homopterans, and dipterans at McNary Dam; and amphipods and dipterans at Bonneville Dam—taxa typical of impounded waters. A series of dams on the Snake and Columbia Rivers has altered the conditions and habitat available for migrating juvenile salmonids and contributed to their decline. Large numbers of hatchery smolts, long residence times, altered food resources, and reservoir morphology may contribute to poor feeding success near Lower Granite Dam and could lead to reduced smolt survival.

Background

Salmonid smolts actively feed during their downstream migration (Becker 1973; Muir and Emmett 1988; Sagar and Glova 1988) to supply needed energy for the rigorous journey that may last many weeks, covering distances of 800 km or more. Metabolism increases during the parr-smolt transformation that accompanies downstream migration (McCormick and Saunders 1987; Farmer et al. 1978) and as water temperatures increase in spring, thus placing further energy demands on smolts.

Hydroelectric dams on the Snake and Columbia Rivers have created slack-water reservoirs that have increased travel times for migrating salmonid smolts, thereby contributing to a decrease in survival (Raymond 1979). Hatcheries have been built to offset losses in wild stocks. In 1993, approximately 81.3 million salmonids were released upstream of Bonneville Dam, of which 16.6 million were released above Lower Granite Dam (Figure 1) (FPC 1994). Yearling chinook salmon (*Oncorhynchus tshawytscha*) of hatchery origin often are released as inadequately developed smolts (Zaugg et al. 1985), a condition resulting in slow migration. For example, yearling chinook salmon released in late March or early April from Dworshak National Fish Hatchery in Idaho, took 3-4 weeks to travel to Lower Granite Dam (Muir et al. 1994). Historically, 3-4 weeks was sufficient for the entire migration to the ocean, 696 km downstream (Raymond 1979). Recent estimates of mortality for hatchery yearling chinook salmon migrating from release site to Lower Granite Dam tailrace have ranged from 21 to 83% (Muir et al. 1995).

In addition to the reduced flows caused by reservoirs, the slack water has led to increased sedimentation. Lower Granite Reservoir contains very fine sediments with high organic content. This sedimentation has led to a benthic community in Lower Granite Reservoir that is low in diversity and dominated by oligochaetes and chironomids (Bennett et al. 1990). Reservoirs downstream from Lower Granite Dam in the Columbia River generally have coarser sediments (Ebel et al. 1989) and greater benthic diversity (Parsley et al. 1989).

The combination of large numbers of hatchery smolts, long residence times, altered food resources, and reservoir morphology may contribute to poor feeding success near Lower Granite Dam. This may lead to decreased smolt condition and eventually to reduced smolt survival. Since hatchery stocks generally enter the reservoir first and reside for an extended period, hatchery

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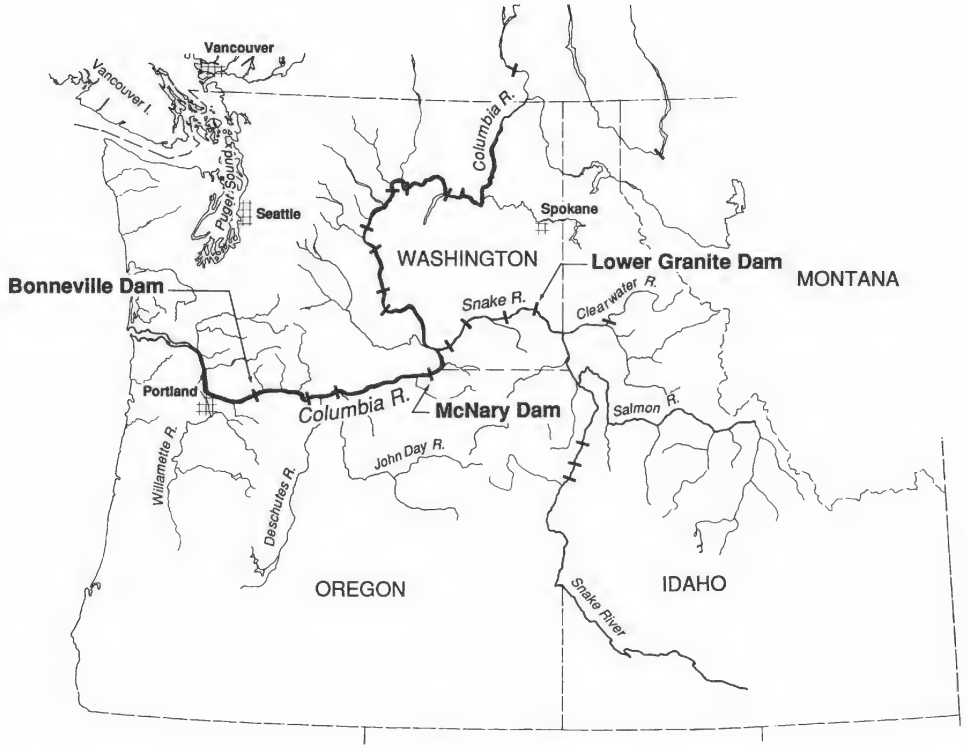

Figure 1. Study area showing location of the three dams (Lower Granite, McNary, and Bonneville) where yearling chinook salmon were sampled for food habit analysis on the Snake and Columbia Rivers.

production could deplete food resources available to later migrating wild smolts, stocks recently listed under the Endangered Species Act (NMFS 1991).

The purpose of this study in 1987 and 1989 was to characterize the food habits of migrating yearling chinook salmon smolts at Lower Granite Dam. Based on the results observed in the first two years, the study area was expanded in 1991 to compare their food habits and feeding success to sites downstream in the Columbia River.

Methods

During 1987 and 1989, freshly killed yearling chinook salmon smolts were collected from a turbine intake at Lower Granite Dam during tests to determine the fish guidance efficiency (FGE) of submersible traveling screens. Fish were taken from fyke nets suspended below the traveling screen to collect smolts passing underneath. Samples were collected between 2000 and 2200 h each evening on four dates in 1987 and three dates in 1989, over the spring smolt migration. Samples sizes varied between years (Table 1).

During 1991, freshly killed smolts were collected from turbine intakes at McNary and Bonneville Dams (Figure 1) once per week during FGE tests. At Lower Granite Dam, no FGE tests were conducted during 1991, so live smolts were sampled from the juvenile fish bypass system as they exited the bypass channel (Matthews et al. 1977). Smolts were sampled simultaneously (same day and time, n = 20 at each site/day), over a 4- to 5-week period during the migration. No attempt was made to distinguish between smolts of wild or hatchery origin, although hatchery fish predominated at all three sites. Yearling chinook salmon were smaller at Lower Granite Dam averaging 124 mm (s.e. 1.3) in fork length compared to 142 mm (s.e. 1.9) at McNary and 142 mm (s.e. 1.6) at Bonneville Dam.

TABLE 1. Sample dates, numbers sampled, number empty (e) and stomach contents (percent IRI) of yearling chinook salmon at three dams on the Snake and Columbia Rivers. Only IRI values >3% are shown. IRI = Index of Relative Importance.

	Sample date		n	e	Dip-tera	Cole-optera	Homop-tera	Hymen-optera	Thysan-optera	Trich-optera	Amphi-poda	Clado-cera	Fish
Lower Granite	1987	Apr 18	10	2	3.5	7.2	—	—	—	—	87.2	—	—
		Apr 24	20	5	—	4.8	—	—	—	6.8	86.5	—	—
		Apr 29	18	3	—	31.5	14.3	—	16.1	—	33.4	—	—
		May 3	20	9	88.4	—	—	—	—	—	11.7	—	—
	1989	Apr 16	104	21	73.0	21.8	—	—	—	—	—	—	—
		Apr 23	67	19	96.4	—	—	—	—	—	—	—	—
		Apr 27	89	28	47.4	4.3	—	—	—	27.0	17.7	—	—
	1991	Apr 25	20	8	—	96.6	—	—	—	—	—	—	—
		May 2	20	6	14.3	13.3	11.8	59.5	—	—	—	—	—
		May 9	20	10	62.7	—	—	29.6	—	—	6.3	—	—
		May 24	20	6	97.4	—	—	—	—	—	—	—	—
McNary	1991	Apr 25	11	2	—	—	—	—	—	—	—	90.9	—
		May 2	20	0	27.6	—	66.9	—	—	—	—	—	—
		May 9	20	0	15.2	—	21.2	—	—	—	—	51.3	8.0
		May 16	20	0	28.4	3.2	41.2	—	—	—	—	17.5	3.5
Bonneville	1991	Apr 25	20	4	63.0	—	—	—	—	—	29.3	—	7.5
		May 2	20	0	38.1	6.6	10.9	36.3	—	—	7.2	—	—
		May 9	20	1	43.7	—	—	—	—	—	55.6	—	—
		May 16	20	0	20.0	4.7	7.4	6.4	—	—	60.7	—	—
		May 24	20	0	11.6	—	3.6	—	—	—	80.9	—	—

To retard digestion of stomach contents, fish stomachs were injected with an 8% formaldehyde solution in 1987 and 1989 or placed on dry ice in 1991 as soon after capture as possible. Later, stomachs were removed and placed in individually labeled vials containing 70% ethyl alcohol for storage.

Stomach contents were identified to the lowest practical taxon (order for insects and species for amphipods). Prey items were weighed to the nearest 0.001 g after blotting and air drying for 10 minutes. When prey items were not intact, head capsules were counted, and body parts were combined for weighing. The number, weight, and frequency of occurrence of food items were used to calculate the Index of Relative Importance (IRI) (Pinkas et al. 1971), converted to percentages for each sample site and date. The percent empty stomachs, and in 1991, mean stomach fullness (Terry 1977) ranging from 1 (empty) to 7 (distended) were calculated for each site each week. Mean stomach fullness values among sample sites for 1991 were compared using the Kruskal-Wallis nonparametric analysis of variance.

Results

During 1987, yearling chinook salmon smolts at Lower Granite Dam ate primarily amphipods (*Corophium spinicorne*) and dipterans (chironomids); during 1989 and 1991, dipterans were the predominant prey item (Figure 2). The proportion of dipterans in the diet generally increased as the yearling chinook salmon downstream migration progressed in time (Table 1). Various terrestrial insect orders including Coleoptera, Homoptera, Hymenoptera, and Thysanoptera also were consumed during the 3 years at Lower Granite Dam (Table 1).

At McNary Dam, yearling chinook salmon smolts preyed primarily on cladocerans, homopterans, and dipterans (chironomids) during 1991 (Figure 3). At Bonneville Dam, amphipods (*Corophium*) and dipterans (chironomids) were the primary food items although hymenopterons and homopterans were also consumed regularly (Figure 3). The proportion of amphipods generally increased as the yearling chinook salmon downstream migration progressed in time at Bonneville Dam (Table 1).

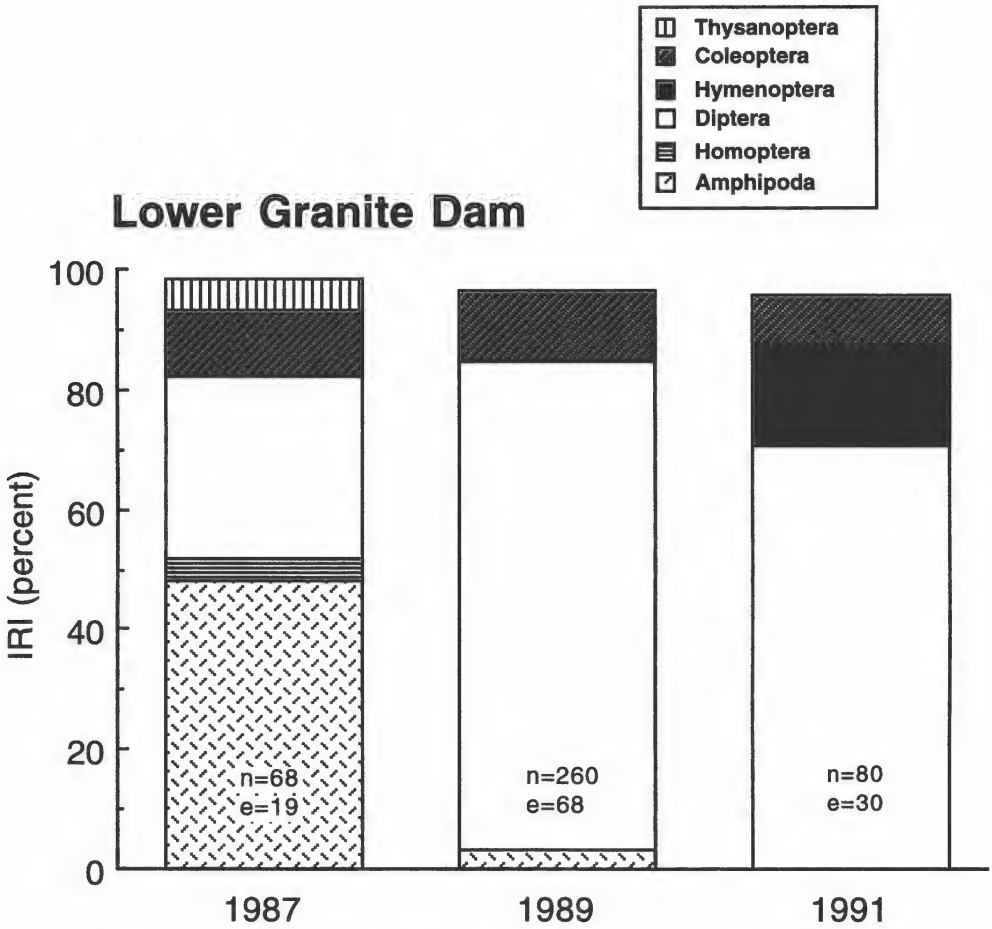

Figure 2. Index of Relative Importance (IRI) of food items for yearling chinook salmon sampled at Lower Granite Dam. Only IRI values > 3% are shown. The number of fish sampled (n) and the number of empty stomachs (e) are also shown.

Yearling chinook salmon smolts collected at Lower Granite Dam did not feed as much as smolts collected at downstream sites. From 1987 to 1991, empty stomachs were observed in 26 to 38% (yearly average) of the yearling chinook salmon smolts sampled at Lower Granite Dam (Figure 2). In 1991, this compared to 3% and 5% empty stomachs (yearly average) in yearling smolts sampled downstream at McNary and Bonneville Dams, respectively, on the Columbia River on the same sample dates and times (Figure 3). Furthermore, mean stomach fullness values were significantly lower ($F = 41.3$, 2 df, $P < 0.0001$) at Lower Granite Dam than at downstream sites in 1991 (Figure 4). Stomach fullness averaged 2.2 at Lower Granite Dam, whereas at McNary and Bonneville Dams, stomach fullness averaged 4.1 and 4.0, respectively.

Discussion

We found that feeding success of yearling chinook salmon smolts collected at Lower Granite Dam was significantly lower than feeding success of smolts collected at downstream sites during 1991. Mean stomach fullness values from McNary and Bonneville Dams during 1991 were similar to levels reported in the lower Columbia River by

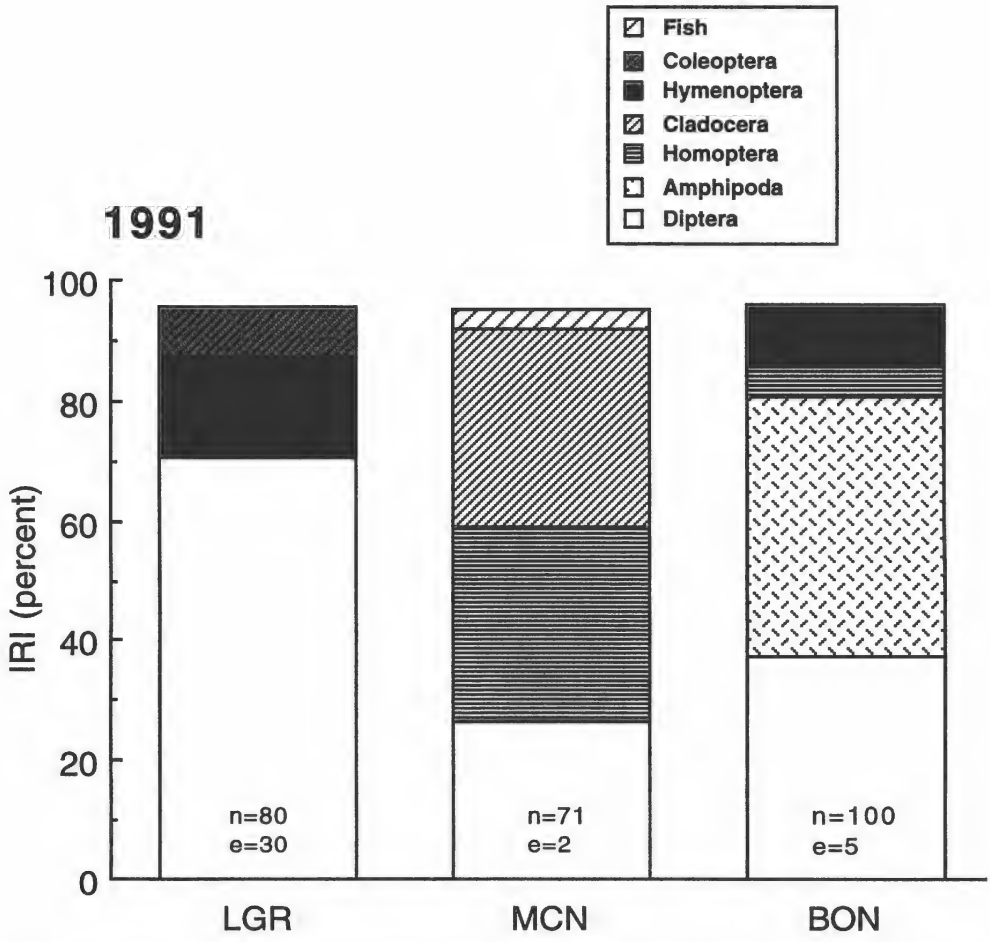

Figure 3. Index of Relative Importance (IRI) of food items for yearling chinook salmon sampled at Lower Granite (LGR), McNary (MCN), and Bonneville (BON) Dams during 1991. Only IRI values > 3% are shown. The number of fish sampled (n) and the number of empty stomachs (e) are also shown.

Dawley et al. (1986), a fullness level they considered inadequate, but still substantially higher than those observed at Lower Granite Dam. Bennett (personal communication, D. Bennett, University of Idaho) found that chinook smolts generally had full stomachs in Lower Granite Reservoir upstream from where fish were collected for this study. A possible explanation for the difference is the morphology of Lower Granite Reservoir. Bennett found shallow water habitat in Lower Granite Reservoir to be important feeding areas for migrating salmonid smolts, and that most of the shallow areas occur in the upper end of the reservoir (Bennett et al. 1990). The lack of shallow feeding sites in the forebay of Lower Granite Dam could be responsible for the lower feeding success observed at this site. Furthermore, yearling chinook salmon may spend considerable time in Lower Granite Dam forebay before they pass the dam. Thorne et al. (1992) determined in a 1989 hydroacoustic survey that the majority of fish in Lower Granite Reservoir accumulate in the forebay area. Thus, fish we collected at the dam may not have eaten for some

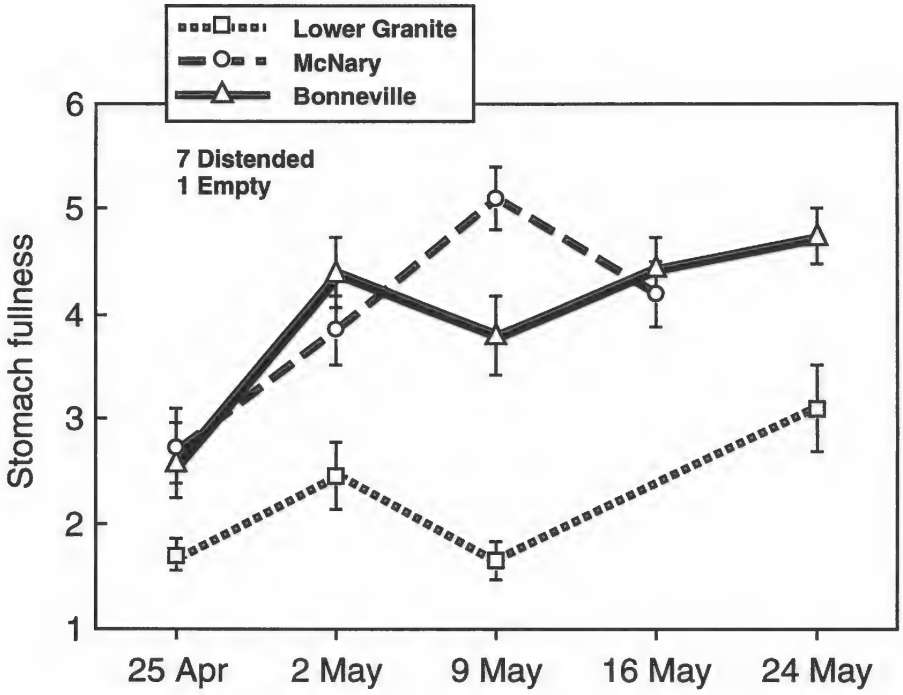

Figure 4. Means stomach fullness in yearling chinook salmon sampled at three dams during 1991 (n=20/site/date except on 25 April at McNary Dam where n=11).

time prior to capture. Similar delays in passage have not been documented at downstream dams.

Salmonids are opportunistic feeders with their diet generally reflecting invertebrate drift availability (Elliot 1967; Sagar and Glova 1988; Rondorf et al. 1990), although some selection occurs (Griffith 1974; Ringler 1979; Sagar and Glova 1987). The difference in overall food habits of fish between dams and between years at Lower Granite Dam probably reflect differences in prey availability.

There is little information on food resources available to migrating salmonids in Snake and Columbia River reservoirs. In Lower Granite Reservoir, Bennett et al. (1990) found chironomids and oligochaetes to be the only abundant organisms in benthic samples. Rondorf et al. (1990) reported cladocerans and terrestrial insects to be the most abundant taxa in zooplankton and insect drift sampling in McNary Dam forebay in summer. Muir (1990) sampled the epibenthic drift just below Bonneville Dam over a three year period and found *Corophium* spp. to be the most abundant drift organisms with highest numbers occurring in May, coinciding with the peak migration of yearling chinook salmon. *Corophium* spp. also were found to be abundant in benthic samples in Bonneville Reservoir (Parsley et al. 1989).

Hatchery salmonids have been found to be ineffective predators immediately after release (Ware 1971; Sosiak et al. 1979; Ersbak and Haase 1983). However, this should not have affected the results observed in this study. The long residence time for yearling chinook salmon in Lower Granite Reservoir should have provided adequate time for adjustment to effectively feed in their new environment. Paszkowski and Olla (1985) determined that coho salmon (*O. kisutch*) smolts switched readily from artificial to natural foods (which they preferred) in a marine environment. Furthermore, hatchery stocks also predominated at Bonneville and McNary Dams, where feeding success was much higher.

With increasing hatchery production and long residence times in Lower Granite Reservoir, the carrying capacity of this reach (or portions of it) may be exceeded, resulting in smolts of poor quality that are unable to resist disease or predation. Starvation could reduce smolt survival by affecting smolt development (Virtanen and Soivio 1985, Fowler 1991), swimming performance (Snyder 1980), making them more susceptible to disease (Snyder 1980), or by impairing fish immune response (Landolt 1989; Henken et al. 1987). This could contribute to the high post-release mortality (Muir et al. 1995) and poor adult returns (Matthews and Waples 1991) reported for hatchery yearling chinook salmon in this reach. There are probably other areas where food availability or potential feeding sites are limited along the Snake and Columbia Rivers migration corridor within the series of impoundments between Lower Granite and Bonneville Dams. The relation between reduced feeding success and migration and survival of yearling chinook salmon is presently unknown and should be examined.

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Equations for Predicting Above-ground Biomass of Plant Species in Early Successional Forests of the Western Cascade Range, Oregon

Abstract

We present a set of 152 regression equations that predict the above-ground biomass of 38 herb, shrub, and tree species common on early successional (clearcut) sites in the western Cascade Range of Oregon. For many of these species, biomass relationships have not been modeled previously or have not been modeled for early successional sites. Biomass of herbaceous taxa is best predicted by cover, while biomass of woody species is best predicted by stem diameter and/or length. We discuss how relationships between biomass and plant size vary with site age among species of diverse growth form and life history. We supplement best-fit models with alternative equations that are easier to implement in the field or that are less sensitive to sources of variation associated with time since disturbance. To minimize the misapplication of equations, we report the dimensional ranges of all plant variables measured, whether or not they are explicitly modeled.

Introduction

There are many ways to sample or compare the relative abundance of plant species. Frequency, canopy cover, stem density, and basal area are commonly used because they are simple to measure or estimate in the field. Where taxa are of similar growth-form (e.g., trees in a forest, graminoids in a meadow), simple measures of abundance may effectively depict the relative importance of species. Where plants are of markedly differing stature, however, simple measures of abundance may provide a poor basis for comparison among species or for describing community-level attributes such as species diversity (Magurran 1988). For example, co-occurring forest herb, shrub, and tree species, each with the same canopy cover, are likely to differ in how they utilize soil water, cycle nutrients, contribute to community structure, or provide resources (food and habitat) for wildlife. Above-ground biomass may, for many purposes, more effectively indicate the relative importance of taxa in such physiognomically diverse communities.

Directly determining plant biomass is labor-intensive, time-consuming, and destructive, requiring harvesting, sorting, drying, and weighing of samples. Such destructive techniques are unacceptable in experimental or long-term studies where plants cannot be removed from sample plots. As an alternative, an indirect, regression approach—allometric or dimensional analysis—is commonly used to predict biomass from attributes that can be measured easily. Dimensional analysis has been applied widely in silviculture and mensuration to estimate tree growth and volume (e.g., Spurr 1952, Walters et al. 1985, Smith 1986, Hann et al. 1987, Husch et al. 1993), and in ecological studies of community structure and function (e.g., Whittaker and Woodwell 1968, Whittaker et al. 1974, Whittaker and Marks 1975, Grier and Logan 1977).

Although it is rarely applied in such situations, the use of dimensional analysis has particular value for predicting plant biomass in permanent plot studies of succession where destructive sampling is not possible, but biomass is an appropriate indicator of dominance. In this paper, we present a set of regression equations for estimating above-ground biomass of plant species common on recent, post-harvest sites in the western Cascade Range of Oregon. The equations were developed for long-term field experiments on species' interactions during succession in *Pseudotsuga menziesii* (Douglas-fir) forests (Halpern et al. 1992, Halpern et al. *in press*). Although early successional change has been well-documented in these forests (Dyrness 1973, Halpern 1988, 1989, Schoonmaker and McKee 1988, Halpern and Franklin 1990, Halpern and Spies 1995), plant biomass has rarely been used to describe the chang-

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ing abundances of species (but see Gholz et al. 1985). This may reflect the paucity of equations available to predict biomass of many plant species (Gholz et al. 1979, Alaback 1986, 1987, Means et al. 1994) and the inherent limitations of these equations.

A problem common to all dimensional analysis is that regression models developed for a particular study may be applicable only to a narrow range of environments, stand ages, plant sizes, or phenological states (Alaback 1986, 1987, Means et al. 1994). Although we do not examine all plant species common to post-harvest sites in the Pacific Northwest, many in our list are widely distributed in western Oregon and Washington. Nonetheless, our equations are most appropriate for low elevation, early successional (1- to 3-yr-old) sites of the central, western Cascade Range of Oregon. Because local environments and plant form change rapidly after forest harvest, for many species we provide separate equations for each successional year.

A second, pervasive problem exists in the literature on dimensional analysis. Authors commonly report the dimensional ranges of the independent variables used in regression equations for the plants destructively sampled, but neglect to document the dimensional ranges of other potentially important variables. For example, the diameter range of the plants used in constructing a diameter-based equation is reported, but the range of stem heights is often omitted. This creates two problems. First, although height may have varied minimally within the harvested population, it may vary in other populations. Second, without knowledge of the full range of plant dimensions for variables other than those utilized in models, it is easy to inappropriately apply equations to other populations. To minimize the potential for misapplication of our equations, we report the dimensional ranges of all variables measured, whether or not they are explicitly used.

Our primary goal is to provide researchers with a set of biomass equations for species that are common after harvest of *Pseudotsuga* forests in the western Cascade Range of Oregon. Biomass relationships for many of these species either have not been modeled previously or have not been modeled for early successional sites. We also illustrate how relationships between biomass and other plant attributes can vary with time among species of diverse growth form and life history. To meet the diverse needs of potential users, we have taken two approaches. First, we identify the independent variable or variables that best predict above-ground biomass for each species. Second, we develop alternative equations for most species that, although less precise, are based on variables that are more easily or quickly measured in the field (e.g., plot-level cover rather than individual stem diameters). Under conditions where precise estimates of biomass are not critical or the best predictors have not been measured, these latter equations can be used with known explanatory power.

Methods

Study Site

Destructive sampling was conducted over a 3-yr period on a clearcut and burned site in which we are studying plant species' interactions during early succession (Halpern et al. 1992, Halpern et al. *in press*). The 4 ha study site lies on a gentle, east-facing slope at 730 m elevation in the Blue River Ranger District of the Willamette National Forest, Oregon, ca. 25 km south of the H. J. Andrews Experimental Forest. Prior to harvest in 1991, the site supported a mature to old-growth forest dominated by *Pseudotsuga menziesii* in the upper canopy and *Tsuga heterophylla* (western hemlock) and *Thuja plicata* (western red cedar) in the lower and sub-canopies. Understories were dominated by *Rhododendron macrophyllum* (Pacific rhododendron), *Gaultheria shallon* (salal), and *Berberis nervosa* (Oregongrape). The forest was clearcut logged in late May and early June 1991 and broadcast burned on 11 September 1991. In Table 1 we present frequency and cover data for species most common in the original forest and for the 3 yr during which we destructively sampled after harvest. Nomenclature follows Hitchcock and Cronquist (1973).

The climate is maritime with mild, wet winters and warm, dry summers. Annual precipitation on the nearby H. J. Andrews Experimental Forest averages 2302 mm, but only 6% falls between June and August (Bierlmaier and McKee 1989). Average minimum temperatures range from -5.5°C in January to 11.9°C in August; average maxima range from 5.5°C in January to 23.3°C in July. The growing season (frost-free period) av-

TABLE 1. Frequency and mean cover of principal plant species on the study site prior to (1990) and for three growing seasons after harvest. Only species with frequencies > 25% for at least one sampling date are listed.

Species	1990 Freq[a] (%)	1990 Cover (SE)[b] (%)	1992 (year 1) Freq (%)	1992 (year 1) Cover (SE) (%)	1993 (year 2) Freq (%)	1993 (year 2) Cover (SE) (%)	1994 (year 3) Freq (%)	1994 (year 3) Cover (SE) (%)
Colonizing Annual and Biennial Herbs								
Cirsium vulgare	0	0.0(0.0)	4	0.2(0.2)	4	t	76	0.5(0.1)
Collomia heterophylla	0	0.0(0.0)	0	0.0(0.0)	16	0.3(0.2)	36	2.1(0.9)
Conyza canadensis	0	0.0(0.0)	0	0.0(0.0)	76	1.5(1.0)	92	4.4(2.2)
Crepis capillaris	0	0.0(0.0)	0	0.0(0.0)	4	t	60	1.4(0.4)
Epilobium paniculatum	0	0.0(0.0)	40	0.6(0.2)	100	26.9(2.3)	100	20.3(4.9)
Lactuca serriola	0	0.0(0.0)	0	0.0(0.0)	36	0.2(0.1)	48	0.9(0.5)
Madia gracilis	0	0.0(0.0)	0	0.0(0.0)	4	t	28	0.3(0.1)
Senecio sylvaticus	0	0.0(0.0)	4	t	100	11.6(1.3)	60	0.3(0.2)
Colonizing Perennial Herbs								
Anaphalis margaritacea	4	t	0	0.0(0.0)	12	t	32	0.3(0.1)
Epilobium angustifolium	4	0.1(0.1)	52	1.0(0.3)	100	6.0(2.3)	96	5.9(2.7)
Epilobium watsonii	0	0.0(0.0)	0	0.0(0.0)	84	0.5(0.2)	80	0.9(0.2)
Gnaphalium microcephalum	0	0.0(0.0)	0	0.0(0.0)	68	0.8(0.5)	100	4.2(1.8)
Lupinus latifolius	4	t	20	0.2(0.1)	40	2.1(1.1)	36	0.8(0.5)
Forest Herbs								
Goodyera oblongifolia	28	0.1(0.1)	0	0.0(0.0)	0	0.0(0.0)	0	0.0(0.0)
Hieracium albiflorum	12	0.1(0.1)	0	0.0(0.0)	12	0.1(0.0)	60	0.4(0.1)
Trientalis latifolia	32	0.3(0.2)	68	0.2(0.1)	72	0.6(0.2)	72	2.0(0.6)
Viola sempervirens	72	3.2(0.8)	48	0.2(0.1)	48	0.9(0.3)	68	0.8(0.3)
Forest Shrubs and Understory Trees (< 1.4 m tall)								
Berberis nervosa	84	26.9(4.4)	64	0.8(0.3)	80	4.7(1.0)	80	7.7(1.9)
Gaultheria shallon	88	39.4(6.2)	24	0.2(0.2)	64	0.6(0.3)	76	1.6(0.4)
Linnaea borealis	72	4.7(1.1)	0	0.0(0.0)	0	0.0(0.0)	4	t
Pseudotsuga menziesii	24	t	0	0.0(0.0)	0	0.0(0.0)	72	0.1(0.0)
Rhododendron macrophyllum	60	40.0(8.5)	16	0.2(0.1)	24	1.8(0.8)	24	2.6(1.3)
Rubus ursinus	36	2.1(0.8)	32	0.7(0.5)	52	4.8(2.0)	60	5.9(2.1)
Tsuga heterophylla	52	4.7(3.1)	0	0.0(0.0)	0	0.0(0.0)	36	t

[a] Frequency of occurrence among sample plots. Pre-harvest (1990) values are based on 225 permanent, 1 m^2 sample plots; post-harvest (1992-1994) values are based on 25 randomly chosen, unmanipulated (control) plots.

[b] Mean canopy cover (with standard error of the mean); t = trace cover (<0.1%).

erages 134 days, but is extremely variable (Bierlmaier and McKee 1989).

Field and Laboratory Methods

We sampled during each of the first three growing seasons (1992-1994) after logging. Plants were harvested on the following dates: 26-30 July and 4-6 August 1992; 23-24 July and 11, 18 and 22 August 1993; and 8-10 August 1994. Two types of plant measurements were taken: (1) measurements of single, above-ground stems to develop individual, stem-based equations, and (2) integrative measurements of species from within 1 x 1 m sample plots to develop plot-based equations. In many instances, plants used to develop stem-based equations were obtained from the same plots used to generate plot-based equations. Minimum sample sizes for most equations were 10 per species; more commonly, 20 or more samples per species were obtained.

We chose independent variables that we anticipated would be good predictors of above-ground biomass and that were fairly easy to estimate or measure in the field. For individual stems, these variables included visual estimates of canopy cover, stem basal diameter measured with a caliper (primarily woody plants), stem length (base to tip), and number of primary shoots (main branches)

per above-ground stem. For plot-level measures, variables included canopy cover, stem density, mean basal diameter of stems (an average of the individual stems measured), and modal stem length (a visual estimate). Because the presence of flowers or fruits influences the relationship between plant size and biomass, we noted the phenological state of all plants; plants were classified as all vegetative, some in flower and/or fruit, and all in flower and/or fruit. Herbivory can also influence plant architecture and the allocation of biomass to foliage, branches and stems. For most species, we observed little direct evidence of herbivore damage, however plants that were obviously browsed were not sampled. Thus, our equations may not be appropriate for sites where herbivory is common.

After plants were measured they were clipped at the ground surface, placed in paper bags, and transported to drying ovens. Samples were dried at ca. 55-60°C for 5-9 days. During this time a subset of the heaviest bags were weighed periodically to insure that stable dry weights were obtained. To minimize absorption of moisture during cooling, paper bags and plants were placed in large plastic bags before they were weighed. All samples were weighed to the nearest 0.01 g.

Analytical Methods

Regression equations were developed using the linear and multiple linear regression procedures of MGLH (Multivariate General Linear Hypothesis) of SYSTAT 5.03 (Wilkinson 1990). We had two primary objectives in our modeling approach: (1) to identify the independent variable(s) that best predicted species' above-ground biomass, and (2) to develop additional equations using variables that are more easily or quickly measured in the field (e.g., plot-level cover rather than stem heights and diameters).

For each species, raw data were graphed to visually assess the relationships between biomass and the independent variables. Using both raw and transformed data, biomass was first modeled as a linear function of each independent variable, followed by stepwise addition of one or more variables if they were shown to be significant (by a t-statistic, $p < 0.05$; Wilkinson 1990). At each step, we examined normal probability plots of residuals, and plots of studentized residuals vs. predicted values to test compliance of the models with the basic assumptions of least-squares regression: that values of the dependent variable are normally distributed about corresponding values of the independent variable, and that the variance of the dependent variable is homogeneous for values of the independent variable (Sokal and Rohlf 1981). Transformations of independent and dependent variables were chosen subjectively using the criteria of Sabin and Stafford (1990). Except for rare cases, logarithmic and square root transformations produced the best models (Appendix 1). Corrections for logarithmic bias were made for log-log equations (Baskerville 1972, Sprugel 1983).

Results and Discussion

A total of 152 regression equations were developed for 38 taxa that are common on early successional, post-harvest sites in the western Cascade Range of Oregon (Appendix 1). The species represent seven broad groups of plants that vary in growth form and successional origin: (1) colonizing annual and biennial herbs, (2) colonizing perennial herbs, (3) colonizing tall shrubs, (4) forest herbs, (5) forest low shrubs and sub-shrubs, (6) forest tall shrubs and understory hardwood trees, and (7) coniferous tree seedlings. For the full set of 152 equations, the median coefficient of determination (R^2) was 0.933 and the range was 0.462-0.997 (Appendix 1). For the 70 primary equations representing the best predictors for each combination of species-by-site age-by-equation type (those with asterisks in Appendix 1), the median R^2 was 0.951 and the range was 0.556-0.997. For each plant group we briefly describe the relationships between plant biomass and form, and how these relationships vary among species and as a function of site age.

The colonizing annual and biennial herbs include winter-annuals that germinate in fall, overwinter as rosettes, and bolt in spring (e.g., *Epilobium paniculatum* and *Senecio sylvaticus*); spring-germinating annuals (e.g., *Conyza canadensis*); and facultative biennials that flower their first year or remain as basal rosettes and flower the second year (e.g., *Cirsium vulgare* and *Lactuca serriola*). Biomass equations were not previously available for a number of these species: *Agoseris grandiflora*, *Conyza canadensis*, *Crepis capillaris*, *Lactuca serriola*, and *Madia gracilis*.

For many taxa in this group, above-ground biomass per stem is predicted well by canopy cover (range of R^2 of 0.671-0.986, Appendix 1), although addition of basal diameter or stem length often improves the relationship (range of R^2 of 0.886-0.986, Appendix 1). However, for some species (*Senecio* and *Conyza* in particular), plant allometry changes with successional time producing different relationships between biomass and cover. For example, stem diameter and height of *Senecio* and *Conyza* decrease with site age (C. B. Halpern, unpublished data) resulting in decreasing plant biomass for a given canopy cover (Figure 1). Consequently, for these species we recommend the use of cover-based equations only on sites with ages similar to those for which equations were developed. Equations that model plant biomass as a function of length and diameter are less responsive to site age (Figure 2) and have R^2 values comparable to cover-based equations (range of 0.814-0.978, Appendix 1). Thus, they have broader applicability. Our results suggest that for most annual and biennial colonists, equations based solely on stem length or basal diameter are poorer than those based on cover. However, for species with greater variation in height than in cover (e.g., *Lactuca serriola*), length is a better predictor of biomass (Appendix 1). The two most common annuals in these early successional communities, *Epilobium paniculatum* and *Senecio sylvaticus*, have been modeled previously (Gholz et al. 1979, Means et al. 1994). Comparability with our equations varies by species, parameter modeled, and site age. For example, our first-year, cover-based equation for *Epilobium* predicts four times the biomass predicted by an equation for an older site (Means et al. 1994). As for *Senecio* and *Conyza*, plants on younger sites (*i.e.* years 1 and 2) have thicker and taller stems than do plants on older sites, resulting in higher plant biomass for a given canopy cover. Predictions of our length-based equations are more comparable with those of Gholz et al. (1979) because length better captures this change in plant allometry with site age.

The group of colonizing perennial herbs includes relatively short-lived species (e.g., *Gnaphalium microcephalum*) and longer-lived taxa that resprout from roots or rhizomes for many years after harvest (e.g., *Epilobium angustifolium*, *Lotus crassifolius*, *Lupinus latifolius*, and *Pteridium aquilinum*) (Halpern 1988, 1989). Biomass equations were not previously available for many of

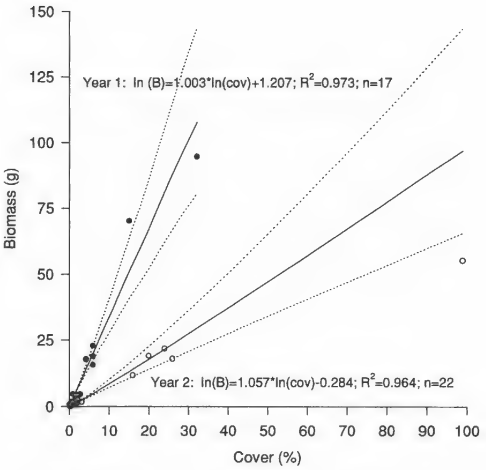

Figure 1. Predicted above-ground biomass (B, in grams) of *Senecio sylvaticus* as a function of plant canopy cover (cov, percentage of a 1 m^2 plot), 1 yr (solid circles) and 2 yr (open circles) after logging and burning. Biomass is plotted only for the range of covers sampled. Dotted lines delimit the 95% confidence intervals. See Appendix 1 for summary statistics and ranges of plant dimensions.

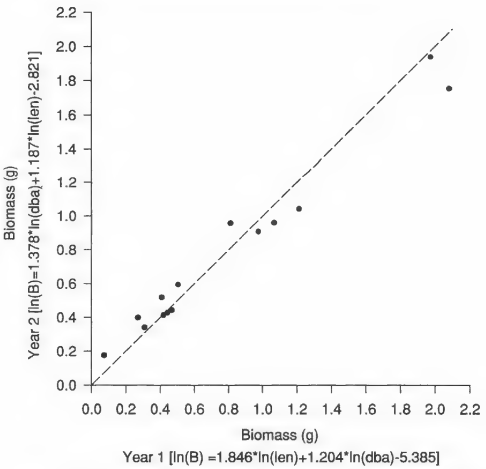

Figure 2. The relationship between the above-ground biomass of *Senecio sylvaticus* predicted for first (X axis) and second (Y axis) year plants. The dashed line is an isoline of equal biomass: that points deviate minimally from this line suggests that biomass predicted by diameter and height varies little between years. The diameters and lengths used to generate the predicted values are from plants measured 3 yr after harvest. See Appendix 1 for summary statistics and ranges of plant dimensions.

these taxa: *Agrostis* spp., *Campanula scouleri*, *Equisetum telmateia*, *Gnaphalium microcephalum*, and *Lotus crassifolius*.

As with the annuals and biennials, variation in the above-ground biomass of colonizing perennials is largely explained by canopy cover (range of R^2 of 0.837-0.991, Appendix 1). The addition of stem length consistently improves the model (range of R^2 of 0.875-0.994, Appendix 1). However, for some species (e.g., the fern *Pteridium aquilinum*; Figure 3), biomass is predicted equally well or better by length than by cover (Appendix 1). Alaback (1987) observed a similar pattern for ferns in southeastern Alaska and attributed the greater explanatory power of length to changes in frond orientation with plant size (*i.e.* fronds orient more vertically as they elongate).

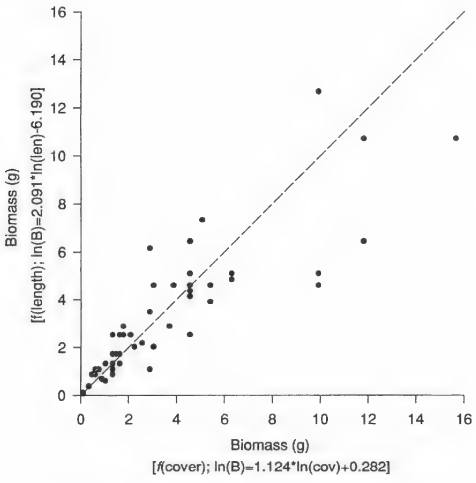

Figure 3. The relationship between the above-ground biomass of *Pteridium aquilinum* predicted by canopy cover (X axis) and total frond length (Y axis). The dashed line is an isoline of equal biomass as a function of cover and length. The values of cover and length used to generate the predictions are those of the 58 individual stems used to develop the models. See Appendix 1 for summary statistics and ranges of plant dimensions.

Several of the perennial herbs in this group (*Epilobium angustifolium* in particular) are extremely plastic in growth form, displaying large variation in height and branching pattern (see ranges for numbers of shoots/plant, Appendix 1). Equations based on cover capture the variation associated with lateral branching, but not the variation associated with changes in allocation to stems and branches or to changes in plant height. Thus, these equations should be applied with caution. For example, it is unclear what accounts for the greater biomass predicted by our equations developed from shorter (1-77 cm tall), first- and second-year plants (Appendix 1) compared with an equation developed for taller plants (14-178 cm) on an older clearcut site (S. Acker and M. Easter, unpublished data).

The group of colonizing tall shrubs are primarily seed bank species that are stimulated to germinate by removal of the tree canopy, physical soil disturbance, or fire. *Arctostaphylos columbiana*, *Ceanothus sanguineus*, *C. velutinus*, *Ribes lobbii*, *Rubus leucodermis*, and *Rubus parviflorus* all belong to genera in which buried seeds lie dormant for periods ranging from decades to centuries (Quick 1956, Gratkowski 1962). Most of the first-year plants sampled were seedlings, although some stems of *Rubus parviflorus* originated from sprouting rhizomes present in locally disturbed sites of the former forest. Biomass regression equations had not been developed previously for *Arctostaphylos columbiana*, *Ribes lobbii*, *Rubus leucodermis*, and *Sambucus cerulea*. For the remaining species, the few existing equations (e.g., Gholz et al. 1979, Means et al. 1994) are inappropriate for small-statured or young plants. Thus, our diameter-based equation for 1- and 2-yr-old *Ceanothus sanguineus* predict half the biomass of that predicted by an equation developed on a site with older, taller stems (Means et al. 1994).

Typically, above-ground biomass of tall shrubs in these forests is best predicted by stem basal diameter (e.g., Gholz et al. 1979, Alaback 1986, Means et al. 1994). With one exception (*Ceanothus velutinus*), the best equations for predicting biomass of colonizing shrubs in our study were based on diameter and/or height (range of R^2 of 0.945-0.997, Appendix 1). Simple cover-based equations are also sufficient for many species in years 1 and 2 (range of R^2 of 0.625-0.990, Appendix 1) reflecting the large proportion of biomass in foliage relative to stem for very young plants. However, cover-based equations should not be applied to plants older than 2 yr.

The group of common forest herbs contains four species that typically occur with high

frequency, but low cover (Table 1). Following harvest they resprout from deep root systems (*Viola sempervirens* and *Hieracium albiflorum*) or tubers (*Trientalis latifolia*), or survive locally in protected microsites (*Galium triflorum*) (McLean 1968, Halpern 1989, J. A. Antos, unpublished data). Existing equations for these species are not specific to early successional sites; rather, they encompass a range of seral stages (Means et al. 1994, S. Acker and M. Easter, unpublished data). Three of the four species show little variation in height, thus, biomass is best predicted by canopy cover (range of R^2 of 0.905-0.985, Appendix 1). For *Hieracium*, which produces a tall flowering stalk from a basal rosette of leaves, cover plus length are the best predictors of biomass.

The group of low-growing forest shrubs includes two typically dominant species, *Berberis nervosa* and *Gaultheria shallon*, and two subordinate sub-shrubs that are often released by removal of the tree canopy, *Rubus ursinus* and *Whipplea modesta* (Halpern 1989). Equations exist for each species (Means et al. 1994), but these represent older clearcut sites or mature forest.

Berberis nervosa and *Gaultheria shallon* show little within-population variation in height during the first, post-harvest growing season, and biomass is adequately predicted by cover (R^2 of 0.980 and 0.956, respectively, Appendix 1). In subsequent years, however, variation in plant height increases. Thus, the addition of modal height improves the model (Appendix 1). Because these sclerophyllous, evergreen shrubs allocate resources to leaves and stems differently under open and closed canopies (e.g., Gholz et al. 1985, Alaback 1986), application of these equations should be limited to clearcut or burned sites of similar age, or to plants of similar stature growing in full-sun conditions. Cover-based equations developed in older clearcuts (Gholz et al. 1979) or mature/old-growth forest (Means et al. 1994, S. Acker, unpublished data) where plants are typically taller, predict significantly higher plant biomass than do our equations.

Rubus ursinus and *Whipplea modesta* are prostrate, stoloniferous taxa that typically show little variation in height; biomass is well predicted by cover (range of R^2 of 0.905-0.985, Appendix 1). For both species, greater predicted biomass with site age (1 vs. 3 yr; Figure 4) suggests that on young, open sites biomass accumulates in woody stems with time. That equations developed for significantly older clearcuts (17-30 yr) or mature forest (145 yr) (Means et al. 1994, S. Acker and M. Easter, unpublished data) predict lower biomass than do our equations suggests that factors other than site age—for example, light availability—affect the accumulation and distribution of above-ground biomass.

The two most common tall shrub and hardwood tree species on our site, *Rhododendron macrophyllum* and *Castanopsis chrysophylla*, are disturbance-tolerant taxa that resprout from adventitious buds at the bases of stems, producing dense, multi-stemmed individuals after logging and burning (Gholz et al. 1985, Halpern 1989). Naturally regenerating *Pseudotsuga menziesii* seedlings were also common. For all three woody species, basal diameter or stem length individually explain most of the variation in stem biomass (range of R^2 of 0.845-0.971, Appendix 1); inclusion of both parameters improves predictions (range of R^2 of 0.895-0.986, Appendix 1). Although biomass predicted by diameter and length are correlated in these species, the strength of this relationship tends to decline with time (e.g., *Rhododendron*, Figure 5) as the allocation of resources to diameter and height growth increasingly vary with time since disturbance. Comparisons with other equations indicate that for stems of equal diameter, predicted biomass increases with site age (*cf.* equations in Appendix 1, Gholz et al. 1979, Means et al. 1994).

Conclusions

Simple measures of plant abundance (canopy cover) or size (stem diameter or length) can be used to accurately predict the above-ground biomass of herb, shrub, and tree species common on early successional sites following harvest of *Pseudotsuga* forests. Biomass of herbaceous taxa is effectively predicted by cover, and biomass of woody species by stem diameter and/or length. Plant form changes rapidly during early succession, thus for many species, equations may differ from year to year. Alternative sets of variables (e.g., diameter plus length rather than cover), or the addition of one or more variables to simpler models, produce equations that are less sensitive to the sources of variation associated with site age or plant form. These results support Alaback's (1987) contention that some of the difficulties in

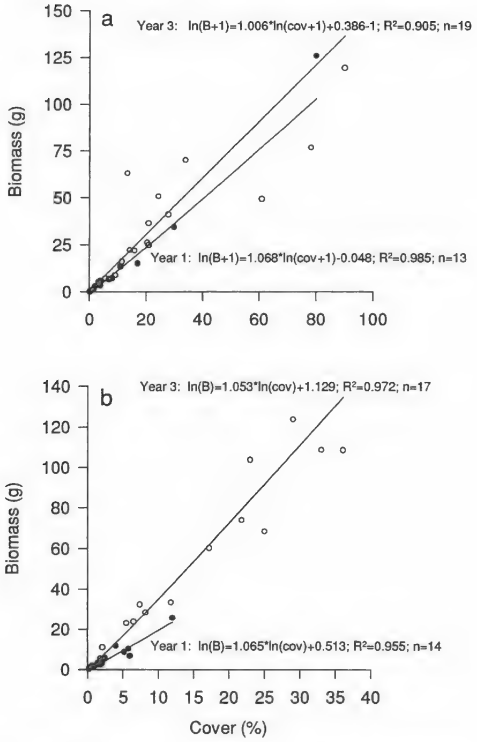

Figure 4. The relationship between total above-ground biomass (B, in grams) and plot-level cover (cov, percentage of a 1 m^2 plot), 1 yr (solid circles) and 3 yr (open circles) after harvest for (a) *Rubus ursinus* and (b) *Whipplea modesta*. See Appendix 1 for summary statistics and ranges of plant dimensions.

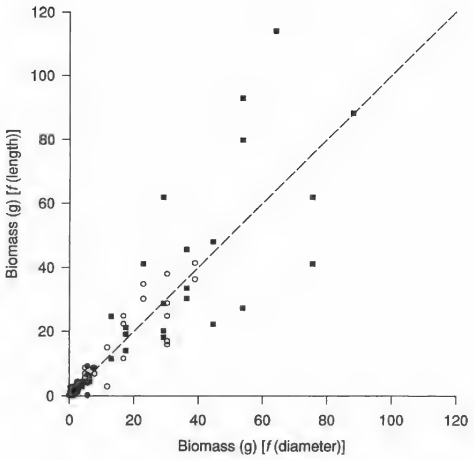

Figure 5. The relationship between the above-ground biomass of *Rhododendron macrophyllum* predicted by stem basal diameter (X axis) and stem length (Y axis), for stems sampled 1 (solid circles), 2 (open circles), and 3 yr (solid squares) after harvest. The dashed line is an isoline of equal biomass predicted by cover and length. The values of diameter and length used to generate the predictions are from the individual stems destructively sampled to develop each model. See Appendix 1 for model form, coefficients, summary statistics, and ranges of plant parameters.

using site- or area-specific regression equations can be overcome by predicting biomass with multiple variables. Additional research is needed to understand how allocation of biomass to foliage, height, and diameter growth vary in response to the rapid changes in physical and biotic environment that characterize early successional sites.

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APPENDIX 1. Equations (with statistics and data ranges) that predict total above-ground biomass of 38 post-harvest plant species. Blanks in data range columns indicate that measurements were not appropriate for the species of interest. Dashes (—) indicate parameter was not measured. Asterisks (*) adjacent to site age denote the primary equations for each species-by-site age-by-equation type (I, P, B) combination—that with the highest coefficient of determination (R^2) (but see footnote j for *Agoseris grandiflora*).

Site age[a]	Type[b]	Equation[c]	R^2	n	MSE	Data range: Cover (%)[d]	Basal diameter (cm)[e]	Length (cm)[f]	No. shoots/plant[g]	Stem density (no./m^2)[h]	P[i]
		Colonizing Annual and Biennial Herbs									
Agoseris grandiflora (large-flowered agoseris)											
3	I	ln(B)=1.223*ln(cov)+0.363	0.873	15	0.236	0.1-1.5		10-30[j]			V
*3	I	sqr(B)=2.314*sqr(cov)-0.513	0.671	20	0.287	0.1-2.1		25-79			VF
3	I	ln(B)=2.826*ln(len)-9.647	0.462	20	0.739	0.1-2.1		25-79			VF
Cirsium vulgare (common thistle)											
*1	I	ln(B)=1.478*ln(cov)+0.053	0.952	11	0.157	0.8-27		2.0-120	1-3		VF
1	I	ln(B)=0.960*ln(len)+0.151	0.857	11	0.465	0.8-27		2.0-120	1-3		VF
Collomia heterophylla (varied-leaf collomia)											
*1	P	ln(B+1)=0.820*ln(cov)+0.717	0.923	18	0.055	0.6-15		—		—	F
Conyza canadensis (horseweed)											
1	I	ln(B)=0.888*ln(cov)+1.266	0.670	27	0.601	0.2-16	0.1-1.1	35-165	1-10		VF
*1	I	ln(B)=0.618*ln(cov)+ 1.783*ln(len)-6.381	0.886	27	0.217	0.2-16	0.1-1.1	35-165	1-10		VF
1	I	ln(B+1)=4.280*ln(dba+1)	0.684	26	0.308	0.2-16	0.1-1.1	35-165	1-10		VF
1	I	ln(B)=2.693*ln(len)-9.679	0.634	27	0.667	0.2-16	0.1-1.1	35-165	1-10		VF
1	I	ln(B)=1.298*ln(dba)+ 1.326*ln(len)-3.177	0.814	26	0.357	0.2-16	0.1-1.1	35-165	1-10		VF
2	I	ln(B+1)=2.988*ln(cov+1)+0.237	0.918	17	0.059	0.1-1.4	0.1-0.8	9-140			VF
*2	I	ln(B)=0.507*ln(cov)+ 1.582*ln(len)-5.516	0.977	17	0.055	0.1-1.4	0.1-0.8	9-140	—		VF
2	I	ln(B)=2.748*ln(dba)+3.222	0.945	25	0.218	0.1-1.4	0.1-0.8	9-140	—		VF
2	I	ln(B)=2.087*ln(len)-8.193	0.963	25	0.148	0.1-1.4	0.1-0.8	9-140	—		VF
2	I	ln(B)=1.145*ln(dba)+ 1.266*ln(len)-3.668	0.978	25	0.092	0.1-1.4	0.1-0.8	9-140	—		VF
*1	P	ln(B)=0.919*ln(cov)+1.132	0.737	24	0.559	0.2-16	0.1-1.1	35-165	1-10	1	VF
Crepis capillaris (smooth hawksbeard)											
*1	I	ln(B)=1.182*ln(cov)+0.086	0.814	12	0.147	0.3-3.0		3.0-57			VF
*3	I	ln(B)=0.674*ln(len)-1.923	0.556	27	0.640	—		1.0-80			VF
Epilobium paniculatum (autumn willow-herb)											
1	I	ln(B)=1.118*ln(cov)+0.351	0.872	24	0.366	0.2-22	0.1-1.0	15-95			VF
*1	I	ln(B)=1.154*ln(cov+1)+ 0.978*ln(dba)+0.451	0.948	23	0.161	0.2-22	0.1-1.0	15-95			VF
1	I	ln(B)=1.815*ln(dba)+ 1.244*ln(len)-1.678	0.899	23	0.312	0.2-22	0.1-1.0	15-95			VF
3	I	sqr(B)=3.597*sqr(dba)-0.821	0.846	29	0.066	—	0.1-0.6	4.0-80			VF
3	I	ln(B)=2.335*ln(len)-8.922	0.930	29	0.307	—	0.1-0.6	4.0-80			VF
*3	I	ln(B)=0.730*ln(dba)+ 1.879*ln(len)-6.206	0.953	29	0.216	—	0.1-0.6	4.0-80			VF
*1	P	ln(B)=1.097*ln(cov)+0.331	0.874	26	0.345	0.2-22	0.1-1.0	15-95		1-2	VF
Lactuca serriola (prickly lettuce)											
2	I	ln(B)=0.655*ln(cov)+1.230	0.494	14	0.459	0.1-1.5	—	13-75	1		VF
*2	I	ln(B)=2.072*ln(len)-7.132	0.861	18	0.178	0.1-1.5	—	13-75	1		VF

Site age	Type	Equation	R^2	n	MSE	Data range: Cover (%)	Basal diameter (cm)	Length (cm)	No. shoots/ plant	Stem density (no./m^2)	P
Madia gracilis (slender tarweed)											
*1	I	ln(B)=0.340*ln(cov)+ 1.823*ln(len)-6.090	0.826	15	0.132	0.6-10	—	34-80			F
Senecio sylvaticus (wood groundsel)											
*1	I	ln(B)=1.003*ln(cov)+1.207	0.973	17	0.090	0.1-32	0.2-1.0	28-85	1-10		F
1	I	ln(B)=0.084*len-3.346	0.809	17	0.632	0.1-32	0.2-1.0	28-85	1-10		F
1	I	ln(B)=1.846*ln(len)+ 1.204*ln(dba)-5.385	0.963	17	0.140	0.1-32	0.2-1.0	28-85	1-10		F
2	I	ln(B)=1.057*ln(cov)-0.284	0.964	22	0.147	0.2-99	0.1-2.1	10-114	—		F
2	I	ln(B)=2.131*ln(dba)+2.528	0.875	23	0.555	0.2-99	0.1-2.1	10-114	—		F
2	I	ln(B)=0.061*len-3.123	0.927	23	0.323	0.2-99	0.1-2.1	10-114	—		F
2	I	ln(B)=0.852*ln(cov)+ 0.493*ln(dba)+0.292	0.972	22	0.121	0.2-99	0.1-2.1	10-114	—		F
2	I	ln(B)=0.761*ln(cov)+ 0.019*len-1.167	0.973	22	0.116	0.2-99	0.1-2.1	10-114	—		F
2	I	ln(B)=1.378*ln(dba)+ 1.187*ln(len)-2.821	0.936	23	0.301	0.2-99	0.1-2.1	10-114	—		F
*2	I	ln(B)=0.696*ln(cov)+ 0.450* ln(dba)+0.540*ln(len)-1.735	0.983	22	0.080	0.2-99	0.1-2.1	10-114	—		F
*1	P	ln(B)=0.986*ln(cov)+1.189	0.974	19	0.087	0.1-32	0.2-1.0	28-85	1-10	1-3	F
*2	P	ln(B)=1.067*ln(cov)-0.449	0.986	10	0.111	0.2-99	0.1-2.1	10-114	—	1-8	F
2	P	ln(B)=2.44*ln(mdba)+ 1.443*ln(num)+2.415	0.955	11	0.402	0.2-99	0.1-2.1	10-114	—	1-8	F
2	P	ln(B)=2.547*ln(mlen)+ 1.055*ln(num)-8.520	0.931	11	0.621	0.2-99	0.1-2.1	10-114	—	1-8	F
Senecio jacobaea[k](tansy ragwort)											
*1	I	ln(B+1)=1.501*ln(cov+1)-0.125	0.914	12	0.114	0.4-22		1.0-20[j]	1		V
Colonizing Perennial Herbs											
Agrostis species (bentgrass)											
*1	P	sqr(B)=1.038*sqr(cov)+0.718	0.886	14	0.193	0.3-20		15-60		1-15	VF
Anaphalis margaritacea (pearly everlasting)											
1	I	ln(B)=1.023*ln(len)+ 1.116*ln(ns)-2.831	0.658	14	0.324	0.4-4.0		7.8-33	1-4		VF
*1	P	ln(B)=1.091*ln(cov)+0.597	0.877	15	0.132	0.4-7.0		7.8-140	1-4	1	VF
Campanula scouleri (Scouler's harebell)											
*1	P	ln(B+1)=1.336*ln(cov+1)+0.119	0.977	12	0.011	0.1-3.5		—		1-15	VF
Epilobium angustifolium (fireweed)											
1	I	ln(B)=1.200*ln(cov+1)-0.212	0.962	26	0.054	0.1-32	—	1.0-77	1-2		V
1	I	ln(B)=1.957*ln(len)-4.850	0.940	26	0.286	0.1-32	—	1.0-77	1-2		V
*1	I	ln(B)=0.827*ln(cov+1)+ 1.319*ln(len)-4.267	0.975	26	0.123	0.1-32	—	1.0-77	1-2		V
2	I	ln(B)=1.865*ln(len)-5.714	0.884	41	0.441	—	—	2.0-49	1-32		V
*2	I	ln(B)=1.719*ln(len)+ 0.451*ln(ns)-5.576	0.918	41	0.321	—	—	2.0-49	1-32		V
1	P	ln(B)=1.266*ln(cov)-0.343	0.949	32	0.241	0.1-72	—	1.0-77	1-2	1-9	V
*1	P	ln(B)=0.757*ln(cov)+ 0.986*ln(mlen+1)-2.837	0.963	30	0.158	0.1-32	—	1.0-77	1-2	1-2	V
2	P	ln(B+1)=1.143*ln(cov+1)-0.008	0.991	18	0.031	0.1-65	—	2.0-73	1-32	1-24	V

Site age	Type	Equation	R^2	n	MSE	Data range: Cover (%)	Basal diameter (cm)	Length (cm)	No. shoots/ plant	Stem density (no./m^2)	P
*2	P	ln(B+1)=1.042*ln(cov+1)+ 0.153*ln(mlen)-0.255	0.994	18	0.021	0.1-65	—	2.0-73	1-32	1-24	V
2	P	ln(B)=1.92*ln(mlen)+ 0.902*ln(num)-5.754	0.984	18	0.202	0.1-65	—	2.0-73	1-32	1-24	V
Epilobium watsonii (Watson's willow-herb)											
*1	I	ln(B+1)=1.432*ln(cov+1)+0.098	0.886	11	0.132	0.1-8.5	—	12-40	—		V
2	I	ln(B)=1.839*ln(len+1)-7.125	0.793	110	0.445	—	—	1.0-80	1-5		VF
*2	I	ln(B)=1.760*ln(len+1)+ 0.774*ln(ns)-6.977	0.806	110	0.422	—	—	1.0-80	1-5		VF
Equisetum telmateia (giant horsetail)											
*1	P	sqr(B)=1.371*sqr(cov)-0.109	0.937	15	0.069	0.2-8.0	—	11-30		1-10	V
1	P	ln(B)=2.496*ln(mlen)+ 1.122*ln(num)-6.802	0.823	16	0.321	0.2-8.0	—	11-30		1-10	V
Gnaphalium microcephalum (white cudweed)											
*1	I	sqr(B)=1.569*sqr(cov)-0.214	0.932	18	0.109	0.1-8.0		3.0-47	—		VF
2	I	ln(B+1)=1.536*ln(cov+1)+0.072	0.969	17	0.096	0.1-25		1.0-73	—		VF
2	I	ln(B)=2.152*ln(len)-5.111	0.950	17	0.651	0.1-25		1.0-73	—		VF
*2	I	ln(B+1)=1.233*ln(cov+1)+ 0.253*ln(len)-0.265	0.987	17	0.043	0.1-25		1.0-73	—		VF
Lotus crassifolius (big deervetch)											
2	I	ln(B)=2.144*ln(dba)+2.582	0.894	22	0.179	—	0.2-1.0	12-76	1		V
2	I	ln(B)=2.112*ln(len)-6.542	0.889	22	0.188	—	0.2-1.0	12-76	1		V
*2	I	ln(B)=1.165*ln(dba)+ 1.097*ln(len)-2.096	0.948	22	0.093	—	0.2-1.0	12-76	1		V
*1	P	ln(B)=0.972*ln(cov)+0.038	0.986	21	0.041	0.2-70	—	6.1-21	1	1-42	V
*2	P	ln(B)=1.124*ln(cov)+0.086	0.986	19	0.071	0.2-100	0.2-1.0	12-70	1	1-16	V
2	P	ln(B)=2.483*ln(mdba)+ 0.846*ln(num)+3.005	0.963	11	0.160	0.2-100	0.2-1.0	12-70	1	1-16	V
2	P	ln(B)=2.47*ln(mlen)+ 1.084*ln(num)-7.291	0.909	19	0.503	0.2-100	0.2-1.0	12-70	1	1-16	V
Lupinus latifolius (broadleaf lupine)											
*1	I	ln(B)=1.282*ln(cov)+0.318	0.962	16	0.182	0.1-32		3.0-55	—		VF
1	I	ln(B)=2.294*ln(len)-5.213	0.888	16	0.545	0.1-32		3.0-55	—		VF
*2	I	ln(B)=1.122*ln(cov)+0.260	0.969	16	0.196	0.1-90		5.0-74	—		VF
2	I	ln(B)=2.471*ln(len)-6.498	0.786	22	1.043	0.1-90		5.0-74	—		VF
1	P	ln(B)=1.230*ln(cov)+0.287	0.960	18	0.196	0.1-32		3.0-55	—	1-2	VF
*1	P	ln(B)=0.907*ln(cov)+ 0.709*ln(mlen)-1.503	0.973	18	0.140	0.1-32		3.0-55	—	1-2	VF
*2	P	ln(B+1)=1.193*ln(cov+1)- 0.041	0.984	21	0.050	0.1-90		5.0-74	—	1-8	VF
Luzula campestris (field woodrush)											
*1	I	ln(B)=1.852*ln(cov)+0.761	0.981	5	0.069	0.2-1.5		3.0-55			F
Pteridium aquilinum (bracken)											
1	I	ln(B)=1.124*ln(cov)+0.282	0.837	58	0.287	0.1-9.0	0.1-0.7	5.0-65			V
1	I	ln(B)=2.091*ln(len)-6.190	0.866	58	0.236	0.1-9.0	0.1-0.7	5.0-65			V
*1	I	ln(B)=0.389*ln(cov)+ 1.415*ln(len)-4.121	0.875	58	0.223	0.1-9.0	0.1-0.7	5.0-65			V
1	P	ln(B)=1.168*ln(cov)+0.318	0.882	36	0.285	0.1-15	0.1-0.7	5.0-60		1-5	V
*1	P	ln(B)=2.113*ln(mlen)+ 0.953*ln(num)-6.164	0.900	36	0.249	0.1-15	0.1-0.7	5.0-60		1-5	V

Site age	Type	Equation	R^2	n	MSE	Data range: Cover (%)	Basal diameter (cm)	Length (cm)	No. shoots/ plant	Stem density (no./m^2)	P
					Colonizing Tall Shrubs						
Arctostaphylos columbiana (bristly manzanita)											
1	I	sqr(B)=1.591*sqr(cov)-0.261	0.956	13	0.010	0.2-1.8	0.1-0.4	5.0-19	1		V
1	I	ln(B)=2.421*ln(dba)+3.506	0.931	13	0.080	0.2-1.8	0.1-0.4	5.0-19	1		V
*1	I	ln(B)=1.398*ln(dba)+ 1.154*ln(len)-0.821	0.963	13	0.047	0.2-1.8	0.1-0.4	5.0-19	1		V
*2	I	sqr(B)=2.671*sqr(cov)-1.569	0.950	11	0.473	2.0-25	0.5-2.1	21-55	1-14		V
2	I	ln(B)=2.025*ln(dba)+3.527	0.901	11	0.100	2.0-25	0.5-2.1	21-55	1-14		V
2	B	ln(B+1)=5.389*ln(bdba+1)- 0.333	0.899	81	0.080	—	0.1-0.9	2.0-50	1-12		V
2	B	ln(B+1)=4.488*ln(bdba+1)+ 0.077*nsb-0.294	0.911	73	0.072	—	0.1-0.9	2.0-50	1-12		V
2	B	ln(B)=2.590*ln(blen+1)-7.149	0.909	81	0.276	—	0.1-0.9	2.0-50	1-12		V
*2	B	ln(B)=2.281*ln(blen+1)+ 0.162*nsb-6.736	0.945	73	0.170	—	0.1-0.9	2.0-50	1-12		V
Ceanothus sanguineus (redstem ceanothus)											
1	I	ln(B)=2.875*ln(dba)+3.134	0.759	11	0.367	0.1-0.9	0.1-0.3	2.0-21	1		V
*1	I	ln(B)=1.888*ln(len)-5.572	0.946	10	0.091	0.1-0.4	0.1-0.3	2.0-17	1		V
2	I	ln(B)=2.476*ln(dba)+2.874	0.823	23	0.466	—	0.1-0.6	3.0-45	1-7		V
2	I	ln(B)=1.878*ln(len)-5.422	0.916	23	0.221	—	0.1-0.6	3.0-45	1-7		V
*2	I	ln(B)=1.588*ln(len)+ 0.173*ns-5.341	0.947	23	0.146	—	0.1-0.6	3.0-45	1-7		V
2	P	ln(B)=0.917*ln(cov)+0.235	0.973	5	0.063	0.2-8.0	0.2-0.4	7.0-30	1-7	1-7	V
2	P	sqr(B)=5.488*sqr(mdba)+ 0.274*num-2.069	0.994	5	0.013	0.2-8.0	0.2-0.4	7.0-30	1-7	1-7	V
*2	P	sqr(B)=0.309*sqr(mlen)+ 1.159*sqr(num)-1.471	0.997	5	0.006	0.2-8.0	0.2-0.4	7.0-30	1-7	1-7	V
Ceanothus velutinus (snowbrush)											
*1	I	B=1.038*cov-0.088	0.847	7	0.005	0.1-0.5	0.1-0.2	3.0-11	1		V
*2	I	ln(B)=0.879*ln(cov)+0.640	0.625	19	0.243	0.3-5.0	0.2-0.6	11-43	1		V
2	I	ln(B)=0.054*len+0.190*ns	0.553	19	0.307	0.3-5.0	0.2-0.6	11-43	1		V
Ribes lobbii (gummy gooseberry)											
1	I	ln(B)=1.261*ln(cov)+0.330	0.908	17	0.235	0.1-11	0.1-0.9	4.0-45	1		V
1	I	ln(B)=2.504*ln(dba)+2.932	0.877	16	0.253	0.1-4.0	0.1-0.5	4.0-45	1		V
1	I	ln(B)=1.829*ln(len)-4.867	0.834	17	0.424	0.1-11	0.1-0.9	4.0-45	1		V
1	I	ln(B)=0.679*ln(cov)+ 1.346*ln(dba)+1.694	0.960	17	0.111	0.1-11	0.1-0.9	4.0-45	1		V
1	I	ln(B)=0.859*ln(cov)+ 0.701*ln(len)-1.716	0.939	17	0.168	0.1-11	0.1-0.9	4.0-45	1		V
*1	I	ln(B)=1.419*ln(dba)+ 0.939*ln(len)-1.032	0.985	16	0.034	0.1-4.0	0.1-0.5	4.0-45	1		V
Rubus leucodermis (black raspberry)											
*1	I	ln(B)=1.285*ln(cov)-0.056	0.990	11	0.040	0.2-15	0.1-1.1	5.0-85	1		V
1	I	ln(B)=2.334*ln(dba)+3.012	0.917	12	0.313	0.2-15	0.1-1.1	5.0-85	1		V
1	I	ln(B)=1.712*ln(len)-4.452	0.915	12	0.319	0.2-15	0.1-1.1	5.0-85	1		V
1	I	ln(B)=1.229*ln(dba)+ 0.884*ln(len)-0.802	0.956	12	0.186	0.2-15	0.1-1.1	5.0-85	1		V

Site age	Type	Equation	R^2	n	MSE	Data range: Cover (%)	Basal diameter (cm)	Length (cm)	No. shoots/ plant	Stem density (no./m^2)	P
Rubus parviflorus (thimbleberry)											
*1	I	ln(B)=2.823*ln(cov+1)-2.216	0.917	21	0.114	0.1-3.5	—	5.0-20	—		V
1	I	ln(B)=2.298*ln(len)-5.500	0.786	21	0.295	0.1-3.5	—	5.0-20	—		V
*1	P	ln(B)=1.240*ln(cov)+0.044	0.935	29	0.149	0.1-21	—	5.0-24	—	1-10	V
Sambucus cerulea (blue elderberry)											
1	I	sqr(B)=1.248*sqr(cov)-0.339	0.942	13	0.011	0.2-2.0	0.2-0.6	3.0-14	1		V
*1	I	ln(B)=1.274*ln(cov)+ 0.636*ln(len)-1.578	0.953	13	0.086	0.2-2.0	0.2-0.6	3.0-14	1		V
1	I	ln(B)=1.891*ln(dba)+ 1.218*ln(len)-1.019	0.913	13	0.157	0.2-2.0	0.2-0.6	3.0-14	1		V
Forest Herbs											
Galium triflorum (sweetscented bedstraw)											
*1	P	ln(B)=0.980*ln(cov)-0.602	0.910	24	0.142	0.1-4.5				1-15	VF
Hieracium albiflorum (white-flowered hawkweed)											
1	P	ln(B)=1.222*ln(cov)+0.559	0.779	21	0.244	0.4-7.0		2.0-110		1-6	VF
*1	P	ln(B)=0.872*ln(cov)+ 0.309*ln(mlen)-0.266	0.905	21	0.111	0.4-7.0		2.0-110		1-6	VF
Trientalis latifolia (western starflower)											
*1	P	sqr(B)=0.873*sqr(cov)+0.054	0.740	14	0.039	0.1-2.4		—		1-18	V
Viola sempervirens (evergreen violet)											
*1	P	ln(B)=0.937*ln(cov)+0.583	0.975	12	0.039	0.1-5.5				1-47	VF
Forest Low Shrubs and Sub-shrubs											
Berberis nervosa (Oregongrape)											
*1	P	sqr(B)=1.698*sqr(cov)-0.340	0.980	21	0.051	0.1-11	—	—	—	1-36	V
3	P	ln(B)=1.161*ln(cov)+1.389	0.937	21	0.212	0.1-30	—	4.5-33	—	1-40	V
*3	P	ln(B)=0.990*ln(cov)+ 0.695*ln(mlen)-0.214	0.955	21	0.161	0.1-30	—	4.5-33	—	1-40	V
3	P	ln(B)=1.546*sqr(mlen)+ 0.164*num-2.764	0.891	21	1.190	0.1-30	—	4.5-33	—	1.40	V
Gaultheria shallon (salal)											
*1	P	ln(B)=1.342*ln(cov)+0.483	0.956	13	0.236	0.1-11	—	—		1-61	V
3	P	ln(B+1)=1.473*ln(cov+1)+ 0.426	0.954	19	0.125	0.1-32	—	2.0-40		—	V
*3	P	ln(B)=1.082*ln(cov)+ 0.629*ln(mlen)-0.017	0.982	19	0.074	0.1-32	—	2.0-40		—	V
Rubus ursinus (Pacific blackberry)											
*1	P	ln(B+1)=1.068*ln(cov+1)- 0.048	0.985	13	0.029	0.2-80				1-42	V
*3	P	ln(B+1)=1.006*ln(cov+1)+ 0.386	0.905	19	0.141	0.3-90				—	V
Whipplea modesta (whipplevine)											
*1	P	ln(B)=1.065*ln(cov)+0.513	0.955	14	0.102	0.2-12				1-34	V
*3	P	ln(B)=1.053*ln(cov)+1.129	0.972	17	0.056	0.6-36				—	V

Site age	Type	Equation	R^2	n	MSE	Data range: Cover (%)	Basal diameter (cm)	Length (cm)	No. shoots/ plant	Stem density (no./m²)	P
						Forest Tall Shrubs and Understory Hardwood Trees					
Rhododendron macrophyllum (Pacific rhododendron)											
1	I	sqr(B)=6.043*sqr(dba)-2.678	0.699	38	0.187	—	0.2-0.8	3.0-35	1		V
*1	I	ln(B)=2.219*ln(len)-5.673	0.947	38	0.126	—	0.2-0.8	3.0-35	1		V
2	I	ln(B)=2.640*ln(dba)+3.413	0.957	31	0.100	—	0.2-1.1	9.0-63	1		V
2	I	ln(B)=2.660*ln(len)-7.299	0.964	31	0.083	—	0.2-1.1	9.0-63	1		V
*2	I	ln(B)=1.237*ln(dba)+ 1.471*ln(len)-2.503	0.981	31	0.044	—	0.2-1.1	9.0-63	1		V
3	I	ln(B)=2.541*ln(dba)+3.130	0.938	32	0.112	—	0.3-1.7	7.0-90	1		V
3	I	ln(B)=0.051*len+0.146	0.915	32	0.153	—	0.3-1.7	7.0-90	1		V
*3	I	ln(B)=1.567*ln(dba)+ 0.021*len+1.876	0.955	32	0.084	—	0.3-1.7	7.0-90	1		V
Castanopsis chrysophylla (golden chinquapin)											
1	I	ln(B)=2.397*ln(dba)+3.289	0.845	23	0.140	—	0.2-0.6	11-50	1		V
1	I	ln(B)=2.397*ln(dba)+3.289	0.845	23	0.140	—	0.2-0.6	11-50	1		V
*1	I	ln(B)=5.411*dba+ 0.025*len-1.969	0.895	23	0.100	—	0.2-0.6	11-50	1		V
						Coniferous Tree Seedlings					
Pseudotsuga menziesii (Douglas-fir)											
1	I	sqr(B)=3.701*sqr(dba)-0.816	0.971	11	0.017	0.1-1.0	0.1-0.7	3.0-24	1		V
1	I	ln(B)=2.355*ln(len)-6.030	0.944	11	0.210	0.1-1.0	0.1-0.7	3.0-24	1		V
*1	I	ln(B)=0.870*ln(dba)+ 1.577*ln(len)-2.903	0.986	11	0.054	0.1-1.0	0.1-0.7	3.0-24	1		V

[a] Site age: number of growing seasons after clearcut logging and slash burning.

[b] Equation type: I = individual stem-based equation, P = plot-based equation. A branch-based (B) equation was developed for *Arctostaphylos columbiana* because it branches profusely from a point at the ground surface after the first growing season.

[c] Predicted biomass, B, is in units of grams/stem (I equations), grams/m² (P equations), or grams/branch (B equations).

[d] Cover (cov): ocular estimate of projected canopy cover (percentage of a 1 m² plot both for individual stem- [I] and plot-based [P] equations).

[e] Basal diameter (dba, mdba, bdba): for individual stem-based (I) equations, the diameter (dba) at the ground surface in centimeters; for plot-based (P) equations, the mean diameter (mdba) of all above-ground stems; and for branch-based (B) equations, the diameter (bdba) of the branch at the point where it joins the main axis of the plant.

[f] Length (len, mlen, blen): for individual stem-based (I) equations, the length (len) of the primary stem from base to tip in centimeters (if phenology = V) or to the tip of the flower or inflorescence (if phenology = VF or F); for plot-based (P) equations, the modal length (mlen) of all above-ground stems (as above for V, VF, and F); for branch-based (B) equations, the length of the branch (blen) from the point where it joins the main axis of the plant to the tip of the branch.

[g] Number of shoots/plant (ns, nsb): number of primary shoots (ns) per above-ground stem; for branch-based (B) equations the number of secondary, or side branches (nsb) per primary branch.

[h] Stem density (num): number of above-ground stems per 1 m² plot; for plot-based (P) equations only. Based on point of emergence from the ground surface.

[i] P: Phenological state; V = all plants vegetative, VF = some plants in flower and/or fruit, F = all plants in flower and/or fruit.

[j] Plants with basal rosettes of leaves only; length is modal leaf length. For *Agoseris grandiflora*, because this equation represents non-flowering plants only, it was not chosen as a primary equation.

[k] Sometimes a biennial or short-lived perennial.

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Snowpack and Runoff Responses to Climatic Variability, Southern Coast Mountains, British Columbia

Abstract

Climatic variability and change occur at a range of time scales and can influence environmental processes and human activity. For example, interannual variations in winter snow accumulation can control water availability for human consumption and hydro-electric generation, while tree-limit may respond to decadal or longer-term shifts in climatic regimes. This study examined variations in temperature, precipitation, April 1 snowpack water equivalent, and annual and summer runoff in the southern Coast Mountains of British Columbia, particularly in relation to interannual and decadal variations in atmospheric circulation over the North Pacific. Temperatures averaged over each winter (November to March) are correlated with the strength of the Pacific North America (PNA) atmospheric circulation pattern as a result of the warm, southerly airflow during enhanced-PNA winters. Winter precipitation is not clearly correlated with the strength of the PNA circulation pattern. However, winters with an enhanced PNA pattern tend to experience more rain and less snowfall, resulting in decreased April 1 snowpack water equivalent. Streamflow response to variations in the strength of the PNA pattern depends on elevation and glacier cover. Following 1976, there was a statistically significant decrease in snowfall, April 1 snowpack and summer runoff from an unglacierized, mountainous catchment. These decreases are consistent with the post-1976 shift toward the strong phase of the PNA pattern during winter which has been documented in the literature.

Introduction

Climatic variability and change can influence environmental processes and human activity. For example, interannual variations in winter snow accumulation can control water availability for human consumption and hydro-electric generation, while the altitudinal limit of tree growth may respond to decadal or longer-term shifts in climatic regimes (Kullman, 1986). An understanding of the nature and causes of climatic variability at a range of time scales can therefore aid in interpreting environmental change and planning resource allocation.

In many areas in the U.S. and Canada, local climatic and hydrologic conditions are related to the strength of the Pacific North America (PNA) circulation pattern over the North Pacific Ocean, especially in winter (e.g. Cayan and Peterson, 1989; Leathers et al., 1991). The PNA pattern is a natural, internal mode of variability in which the strong phase is characterised by southerly air flow along the west coast with a ridge of high pressure over the Rocky Mountains; westerly zonal flow dominates the weak phase (Wallace and Gutzler, 1981). The strong phase of the PNA pattern in winter appears to be favoured when sea surface temperatures (SSTs) in the equatorial Pacific are above normal, and it is therefore related to the El Niño-Southern Oscillation (ENSO) phenomenon (Trenberth and Hurrell, 1994). An understanding of the relations between local climate and circulation patterns can provide a basis for interpreting past hydroclimatic variability (Trenberth, 1995), for "down-scaling" output from General Circulation Models (GCMs) to generate predictions of the local consequences of global climatic change (Matyasovszky and Bogardi, 1996), and potentially for forecasting water supply with lead times of one to two seasons ahead (Cayan and Peterson, 1989).

Many previous studies of hydroclimatic variability have examined relatively extensive areas, such as the western U.S. (Redmond and Koch, 1991) and British Columbia, Canada (Moore and McKendry, 1996). The present study documents variations in local climate, snowpack water equivalent and streamflow in a more restricted region, the southern Coast Mountains of British Columbia. This study adds to and builds on previous studies within the Pacific Northwest (e.g. Greenland, 1995), and contributes to a more detailed regional picture of climatic variability and its environmental consequences. This study addresses two questions: (1) are interannual variations in snowpack and streamflow related to the strength of the winter PNA circulation pattern, and (2) is there evidence of the climate-related step change beginning in 1977 which was documented by Trenberth (1990) and Ebbesmeyer et

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al. (1991). Winter is defined here as comprising the months November to March, inclusive, as opposed to at least one study that defined a winter half-year as October to March (Redmond and Koch, 1991). The November-March period is used here because it better represents the period of major snow accumulation, and it is the period when "winter" circulation patterns are best expressed (Trenberth, 1990).

The Study Area

This study focuses on the southern Coast Mountains and adjacent portions of the Cascades north of the Canada-U.S. border (Figure 1). The Coast Mountains rise to over 3000 m elevation. The glaciation limit varies from about 1900 m in the western, maritime-influenced areas to 2700 m in the eastern portions of the Coast Mountains (Østrem, 1966). Mean annual precipitation varies with elevation, but ranges from over 4000 mm in the west to less than 1000 mm in the east. Over 60% of mean annual precipitation falls between November and March. Treeline occurs between about 1500 and 2000 m.

The study area includes the Greater Vancouver Regional District (GVRD), which has a rapidly growing population and demand for water. The water supply for the GVRD depends on the spring snowpack to provide reservoir inflows through the spring and summer. Water use restrictions have been applied in years in which a dry summer has followed a winter with low snow accumulation

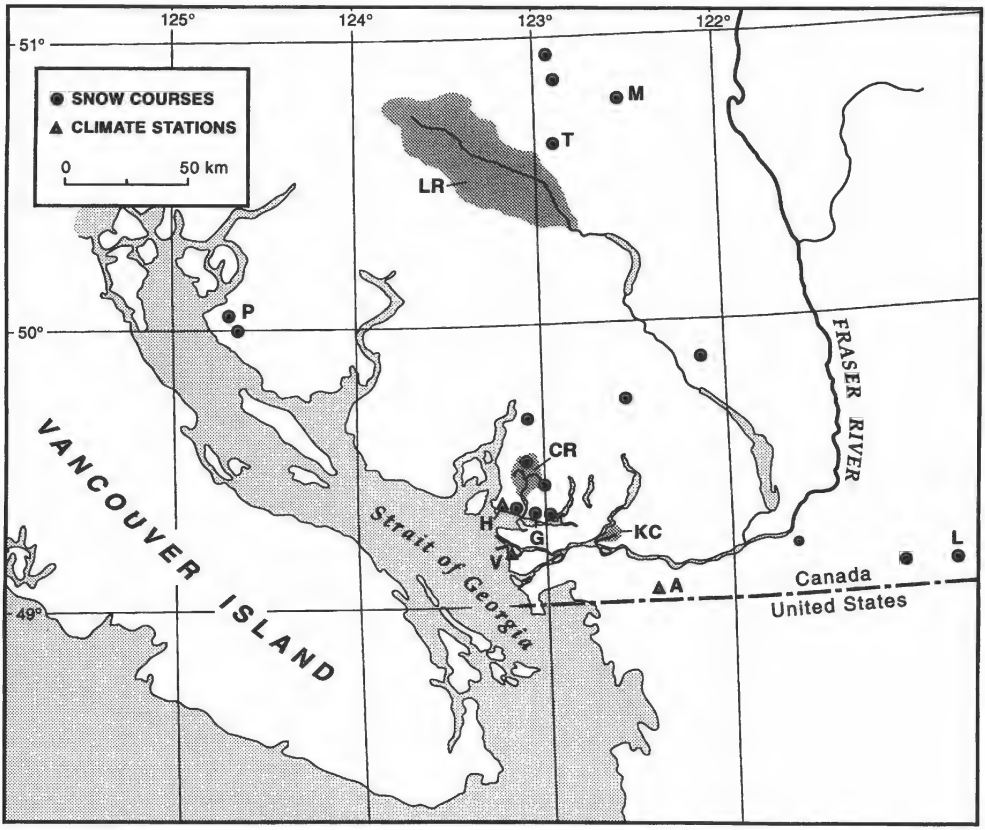

Figure 1. Map of study area, showing station locations. Letter codes identify stations referred to in the text and/or figures: A, Abbotsford Airport; CR, Capilano River; G, Grouse Mountain; H, Hollyburn; KC, Kanaka Creek; L, Lightning Lake; LR, Lillooet River; M, McGillivray Pass; P, Powell River (Upper and Lower); T, Tenquille Lake; V, Vancouver Airport.

(e.g. 1992). The winter snowpack also provides an important resource for both resort-based and back-country recreation.

Methods

Atmospheric Circulation

The values of the NP index described by Trenberth and Hurrell (1994), averaged over each November-March period, were used as an index of the strength of the PNA circulation pattern during winter. The NP index is the area-weighted average sea level pressure over the region from 30 to 65°N and from 160°E to 140°W. The NP index is highly correlated with the PNA index of Wallace and Gutzler (1981) (r = -0.91), and is believed to be a more robust index of atmospheric circulation over the North Pacific (Trenberth and Hurrell, 1994). Figure 2 shows the time series of NP. Low values of NP correspond to winters with an enhanced PNA pattern, high values to winters with dominantly zonal airflow over the North Pacific.

Hydroclimatic Data

Analysis of network hydroclimatic data always involves compromising between spatial coverage and length of record. In this study, stations were chosen that had at least 9 years of record prior to the 1977 step change, to provide some representation of the earlier regime.

Monthly temperature and precipitation data were obtained from the Atmospheric Environment Service. Three stations met the criterion that there had to be no station re-locations or other obvious sources of discontinuity in the record. Station locations are shown on Figure 1. Station elevations are: Vancouver Airport, 3 m; Abbotsford Airport, 58 m; and Hollyburn Ridge, 951 m. Mean temperatures and total snowfall, rainfall and precipitation were calculated for each November-March winter period.

April 1 snow course data were obtained from the B.C. Ministry of Environment. Each value represents the average snowpack water equivalent (SWE) based on 5 to 10 snow cores.

Streamflow data were obtained from Water Survey of Canada. Stations were selected which had natural flow conditions or minimal regulation. Runoff was calculated for each water year (October to September), as well as for each summer half-year (April to September). The three catchments meeting the selection criteria, shown in Figure 1, represent a range of hydrologic regimes found within the region. Kanaka Creek's catchment has a peak elevation of 920 m and is dominated by winter rainfall. Capilano River's basin has a peak elevation of about 1750 m and in many years has a substantial seasonal snowpack which lasts into spring and early summer. The drainage area for Lillooet River has 17% glacier cover and has peak elevations up to 3120 m. Most winter

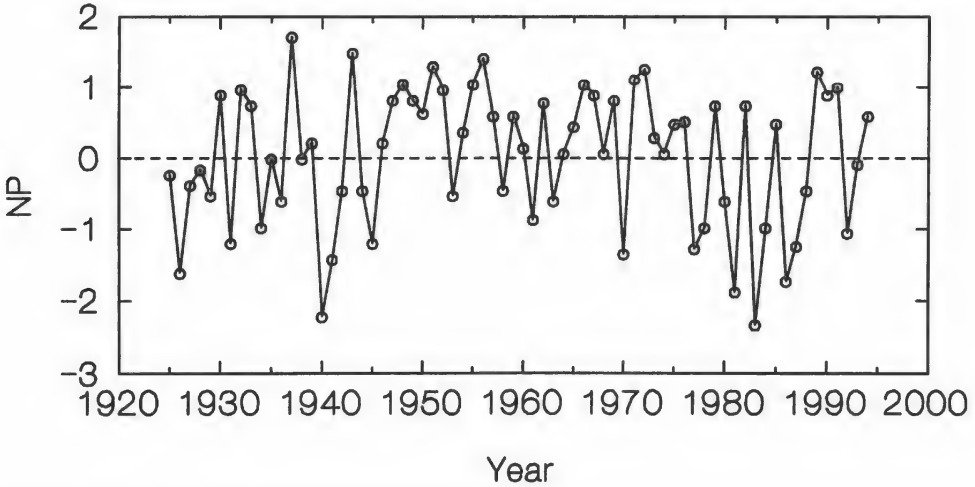

Figure 2. Time series of Trenberth's North Pacific (NP) index.

precipitation in the Lillooet catchment falls as snow which melts in the spring and summer.

The Greater Vancouver Water District regulates Capilano River flows by draining a mountain lake to augment late-summer low flows. However, under normal operations the volume of water released would be at most equivalent to 56 mm of runoff, or about 3.5% of the mean summer runoff of 1575 mm (for the period 1961-1992). The effects of this regulation on interpretation of the analyses will be considered in the discussion.

Data Analysis

The relations between hydroclimatic elements and the NP index were assessed by examination of scatterplots and calculation of Spearman's coefficient of rank correlation. The use of rank correlation helps accommodate possible non-linearity in the relations as well as violation of the assumption of bivariate normality (Steele and Torrie, 1980, p. 550). The existence of a step change beginning in 1977 was tested by splitting the data into two periods, one from 1961 to 1976 and the other from 1977 to 1992 (which is when many of the data series end). Student's t statistic was used to test the null hypothesis that there was no change in the mean value between the earlier and later periods. Only stations having relatively complete records (fewer than 10% missing values) for the period 1961 to 1992 were included in this analysis. This criterion maximizes the sample size and provides approximately equal sample sizes in the two periods, thereby maximizing the power and robustness of the t test in the face of possible non-normality and heteroscedasticity of the parent distributions (Zar, 1984, p. 137).

It should be noted that the significance levels indicated by the value of a test statistic are valid in the case of one comparison. Where multiple tests are conducted, as in this study, the risk of incorrectly rejecting the null hypothesis will exceed the calculated significance level for a single test. Therefore, in interpreting the analyses, emphasis will be placed on consistency of trends amongst the variables as well as on the apparent statistical significance of the trends.

Results

Temperature and Precipitation

Seasonal temperatures and precipitation at Vancouver Airport are generally correlated with those at the other two stations, especially Abbotsford Airport. Time series of Vancouver Airport data are shown in Figure 3. Although there is no obvious trend in winter temperatures, years with low values of NP generally coincided with warm winters (e.g. 1970, 1977, 1981, 1983). This correlation is also apparent in Figure 4 and Table 1. There is no clear association between winter total precipitation and NP (Table 1, Figure 5). Some years of enhanced PNA circulation (low NP) had low precipitation (e.g. 1970, 1977) while others had high precipitation (e.g. 1981, 1983). Unlike total winter precipitation, snowfall is significantly correlated with NP (Table 1, Figure 5, Figure 6).

Student's t tests revealed no significant differences in winter temperatures or total precipitation between the two periods (Table 2). Summers in the 1977-1992 period were significantly warmer by about 0.5°C, at least at the lower elevation stations (Hollyburn Ridge had too many missing values for this analysis). A summer warming trend appears to have started in 1977 (Figure 3). Winter snowfall was substantially lower in the 1977-1992 period at the two lower-elevation stations, but the difference is not quite significant at the 95% confidence level at Abbotsford Airport. This marginal lack of significance may be caused by the fact that winter snowfall in a given year at the low elevation stations can be dominated by one or two events, leading to great interannual variability.

TABLE 1. Spearman's coefficient of rank correlation (r) between climatic data and the NP index (T_w = winter temperature; P_w = winter precipitation; S_w = winter snowfall).

	Hollyburn Ridge			Vancouver Airport			Abbotsford Airport		
	T_w	P_w	S_w	T_w	P_w	S_w	T_w	P_w	S_w
r	-0.66	0.21	0.74	-0.67	0.07	0.71	-0.61	0.24	0.66
n	26	34	34	55	54	50	45	46	46
p-value[1]	<0.01	ns	<0.01	<0.01	ns	<0.01	<0.01	ns	<0.01

[1]ns indicates $p > 0.05$.

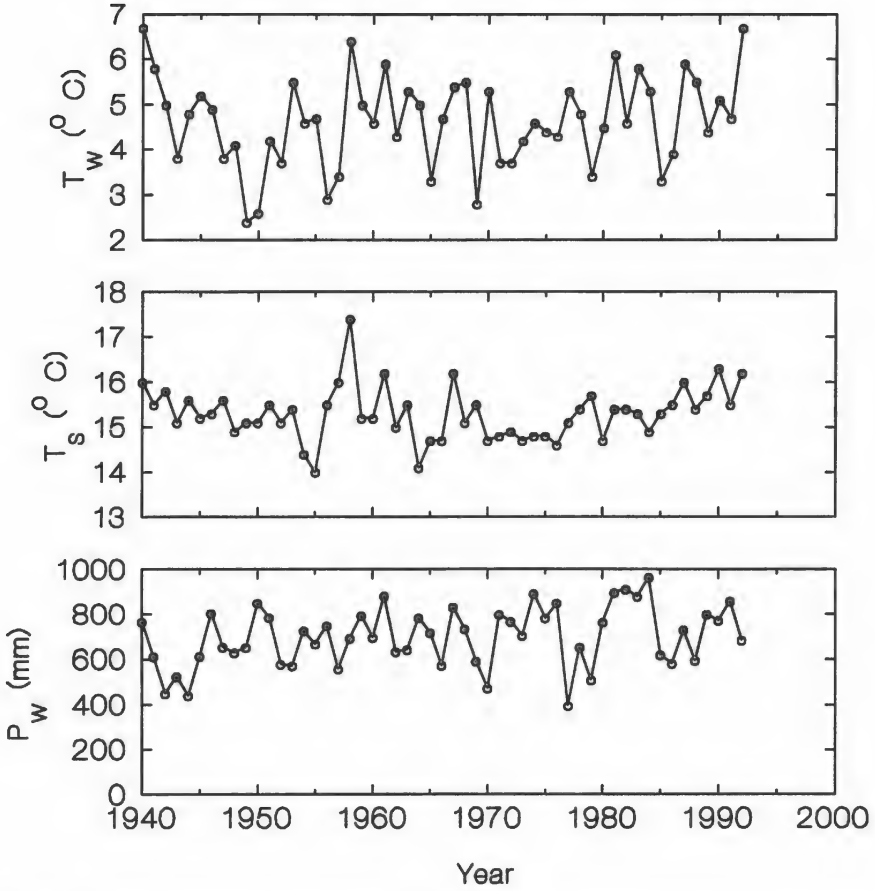

Figure 3. Time series of winter temperature, summer temperature and winter precipitation at Vancouver Airport.

April 1 Snowpack Water Equivalent

All of the stations analysed for a step change experienced lower average SWE following 1976 (Table 3). Decreases relative to the 1961-1976 mean averaged 31%. The smallest decreases (16% to 25%) occurred at stations located between the Lillooet and Fraser Rivers, where the maritime influence is weaker and station elevations are highest. At seven of the stations the decrease had significance levels of about $p = 0.01$ or less, while the shift at the eighth station, McGillivray Pass, was not quite significant with $p = 0.054$. Figure 7 shows time series for selected stations.

Rank correlation coefficients between SWE and NP ranged from 0.30 to 0.73. Correlation coefficients tended to be lower for stations between the Fraser and Lillooet Rivers (0.30 to 0.47). Of the 17 stations included in the analysis, only one, McGillivray Pass, had a correlation which was not quite significant ($r = 0.30$ and $p \approx 0.06$). Figure 8 illustrates the SWE-NP relation for selected stations.

Runoff

Annual runoff decreased for all three rivers by 6% to 11% relative to the 1961-1976 means. However, these decreases are not significant at $\alpha = 0.05$ (Table 4). The only statistically significant change was for summer runoff for Capilano River, which decreased 18% following 1976 (Figure 9).

TABLE 2. Results of Student's t tests for climatic data.

	Vancouver Airport				Abbotsford Airport			
	T_w	T_s	P_w	S_w	T_w	T_s	P_w	S_w
Change[1]	0.43°C	0.47°C	-3 mm	-36 mm	0.35°C	0.49°C	-81 mm	-40 mm
change[2]			-0.4%	-51%			-8%	-43%
t	1.35	2.64	-0.06	-2.25	0.9	2.38	-1.14	-1.95
p-value	0.19	0.01	0.95	0.03	0.36	0.02	0.26	0.06

[1] mean for 1977-1992 - mean for 1961-1976

[2] for precipitation and snowfall, change as a percentage of the 1961-1976 mean

TABLE 3. Results of analyses for snowpack data. Sub-regions are defined as follows: (1) Coast Mountains west of Lillooet River; (2) Coast Mountains east of Lillooet River; (3) Cascade Range.

			Results of t test			Results of correlation analysis		
Station	Elevation (m)	Sub-region	Change (%)	t	p-value	r	n	p-value[1]
Grouse Mountain	1100	1	-42	3.90	<0.001	0.51	57	<0.01
Palisade Lake	880	1	-37	3.38	0.002	0.46	46	<0.01
Dog Mountain	1080	1	-34	2.97	0.006	0.56	48	<0.01
Powell River Lower	910	1				0.73	35	<0.01
Powell River Upper	1040	1				0.67	32	<0.01
Hollyburn	1100	1				0.40	43	<0.01
Loch Lomond	900	1				0.51	37	<0.01
Mount Seymour	1070	1				0.65	30	<0.01
Stave Lake	1210	1				0.56	25	<0.01
Tenquille Lake	1680	2	-20	2.76	0.010	0.32	40	<0.05
McGillivray Pass	1800	2	-16	2.01	0.054	0.30	40	ns
Green Mountain	1630	2	-25	2.80	0.009	0.45	30	<0.05
Bralorne	1450	2				0.47	30	<0.01
Nahatlatch River	1520	2				0.42	25	<0.05
Wahleach Lake	1400	3				0.72	25	<0.01
Lightning Lake	1220	3	-29	3.30	0.003	0.54	45	<0.01
Klesilkwa	1130	3	-43	2.39	0.024	0.71	45	<0.01

[1] ns indicates $p > 0.05$

Table 5 summarizes the correlations between annual and summer runoff and NP. None of the correlations for annual runoff is significant. For summer runoff, only Capilano River has a significant correlation with NP. Figure 10 illustrates runoff-NP relations for Capilano River.

Table 6 shows that, although summer runoff for Lillooet River is more highly correlated with variations in spring snow accumulation, summer temperatures at Vancouver Airport also account for a significant proportion of the variance of summer runoff. The correlation between Lillooet River's summer runoff and air temperature results from contributions of glacier melt, which is positively correlated with summer air temperatures (Collins, 1987).

Discussion

The weak correlations between winter precipitation and NP found in this study are not consistent with those reported for adjacent areas in the U.S. Pacific Northwest by Redmond and Koch (1991), who found highly significant negative correlations between October-March precipitation and

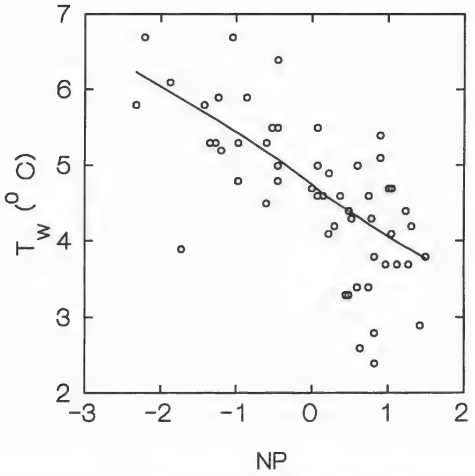

Figure 4. Scatterplot of winter temperature at Vancouver Airport against the NP index. The smoothed fits in this and following figures were calculated using the LOWESS algorithm (Cleveland, 1979).

a PNA index for the period 1947-48 through 1983-84. The difference cannot be explained by the use of November-March as an integrating period in this study: the correlation between October-March total precipitation at Vancouver Airport and October-March average NP is 0.141, which is not statistically significant at the 0.05 significance level. The weak correlation probably reflects the relatively heavy precipitation during some enhanced PNA years, particularly 1981 and 1983. Moore and McKendry (1996) found weak correlations between winter precipitation and NP, and the occurrence of heavy precipitation in 1981 and 1983, for several stations in southern British Columbia. Stations in Washington such as Concrete, on the other hand, received relatively light precipitation in 1981 and 1983 (Harper, 1993), consistent with the results of Redmond and Koch (1991). Further research should investigate the nature and causes of precipitation variability in the Pacific Northwest region.

TABLE 4. Results of Student's t tests for streamflow data

	Kanaka Creek		Capilano River		Lillooet River	
	annual	summer	annual	summer	annual	summer
change[1]	-169 mm	10 mm	-419 mm	-305 mm	-117 mm	-81 mm
change[2]	-9%	2%	-11%	-18%	-6%	-5%
t	-1.08	0.2	-1.75	-2.75	-1.60	-1.47
p-value	0.29	0.84	0.09	0.01	0.12	0.15

[1] mean for 1977-1992 - mean for 1961-1976 (mm)

[2] change as a percentage of the 1961-1976 mean

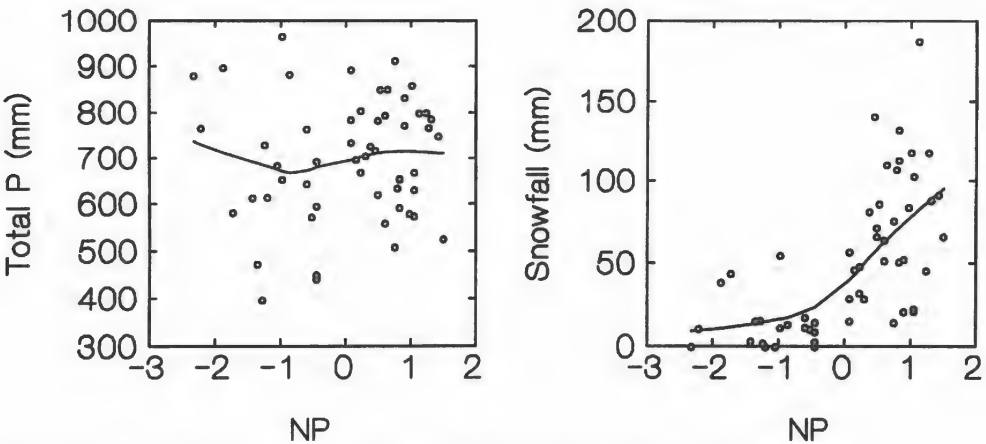

Figure 5. Relations between winter total precipitation and snowfall at Vancouver Airport and the NP index.

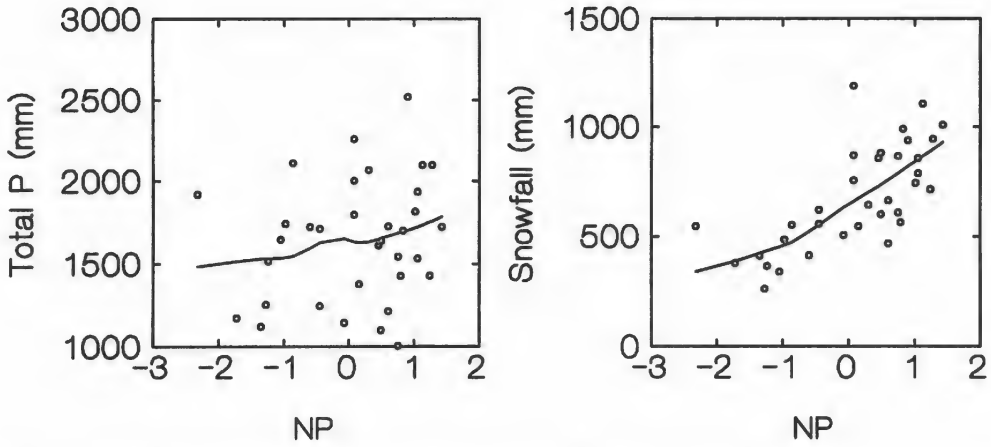

Figure 6. Relations between winter total precipitation and snowfall at Hollyburn Ridge and the NP index.

TABLE 5. Spearman's coefficient of rank correlation between streamflow and the NP index.

	Kanaka Creek		Capilano River		Lillooet River	
	annual	summer	annual	summer	annual	summer
r	0.34	0.08	0.03	0.47	0.07	0.08
n	31	32	64	65	64	67
p-value	ns	ns	ns	<0.01	ns	ns

TABLE 6. Regression analysis of Lillooet River summer runoff as a function of April 1 SWE at Tenquille Lake and Vancouver Airport summer temperature.

Fitted equation	$\tilde{R}^2$	df	s.e.	p
$\hat{Q} = -380 + 119 \cdot T_s$	0.20	38	149	0.002
$\hat{Q} = 1017 + 0.356 \cdot SWE$	0.34	38	135	<0.001
$\hat{Q} = -943 + 0.372 \cdot SWE + 127 \cdot T_S$	0.58	37	108	<0.001

$\hat{Q}$ = predicted summer runoff (mm)
$\tilde{R}^2$= coefficient of determination adjusted for degrees of freedom
df = degrees of freedom
s.e. = standard error of the estimate (mm)

The negative correlation between winter temperatures and NP is consistent with previous studies, and results from the advection of warm, southerly air along the North American west coast during periods of enhanced PNA circulation (Leathers et al., 1991). During storms, the warmer temperatures would produce higher freezing levels and therefore more rain and less snow, even at higher elevations. The generally lower snowpack water equivalent associated with enhanced PNA circulation is caused by this freezing level effect in wet winters such as 1980-81 and 1982-83, rather than by lack of precipitation as was the case in 1969-70 and 1976-77. However, in the lee portion of the Coast Mountains (i.e. between the Lillooet and Fraser Rivers), the weaker maritime influence would have depressed freezing levels relative to areas nearer the coast. These depressed freezing levels, combined with the higher station elevations in the lee side (Table 3), probably account for the weaker SWE-NP correlations observed there.

Streamflow variations are consistent with the temperature, precipitation and snowpack data. At Kanaka Creek and Capilano River, where annual storage changes are minimal, the lack of correlation between annual runoff and NP reflects the

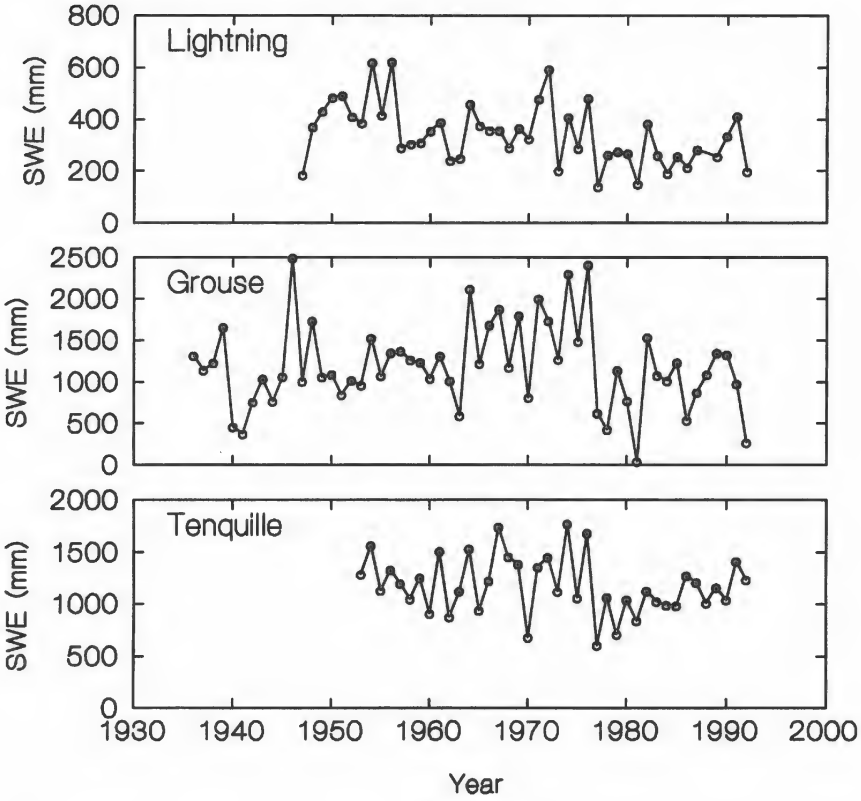

Figure 7. Selected time series of April 1 snowpack water equivalent.

fact that precipitation is not correlated with NP. However, summer runoff at Capilano River is positively correlated with NP, because in years with an enhanced PNA pattern (low NP), there is more rain and less snowfall, and therefore more of the runoff occurs in winter and less during the following spring and summer. The correlation between summer runoff and NP is likely understated by the data, since flow augmentation would tend to be greater following low snowpack (low NP) winters, effectively reducing the contrast in summer runoff following low- and high-NP winters. The lack of correlation between summer runoff and NP at Kanaka Creek reflects the low elevation of its catchment, and the consequent lack of a significant snowpack.

The lack of correlation with NP for both annual and summer runoff for Lillooet River is due to the effects of glacier melt. The increased summer temperatures since 1976 have likely produced more glacier melt, tending to offset the decrease in runoff from seasonal snowmelt. However, many glaciers in the south Coast Mountains and adjacent U.S. Pacific Northwest currently have a negative mass balance (Brugman, 1992; Pelto, 1996). If the current climatic regime continues, the effects of glacier melt will eventually diminish as the glaciers recede.

Generalization of these results within the study region must be tempered by consideration of the limitations of data coverage. The climate stations represent the weakest coverage, and only sample the maritime edge of the region. The snow courses are better distributed across the region, but not necessarily with elevation. The snow courses west of the Lillooet River and in the Cascades sample the zone below about 1200 m elevation, while those east of the Lillooet River sample the zone

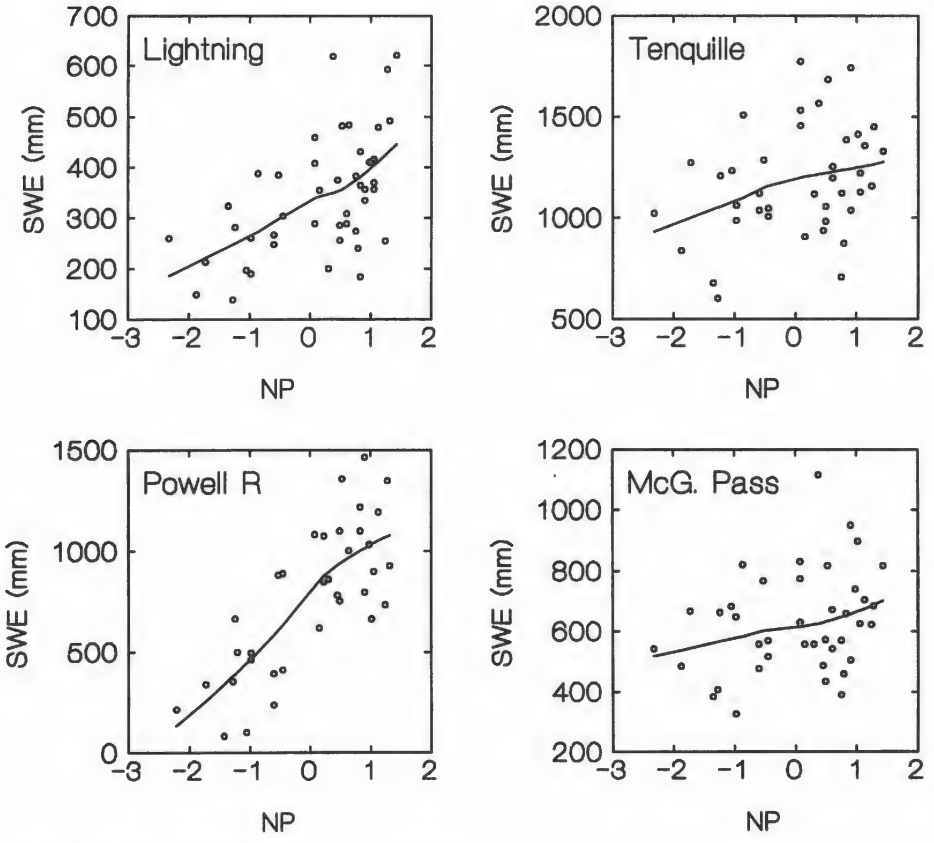

Figure 8. Scatterplots of SWE vs. NP for selected stations.

above 1400 m. In terms of streamflow data, there is only one catchment for each of the flow regimes (i.e. winter rainfall, winter rainfall/spring snowmelt, and spring-summer snow/glacier melt). Despite these considerations, the consistency of trends amongst the variables indicates that the regional-scale relations between surface hydroclimate and atmospheric circulation are probably real.

Trenberth (1990) and Ebbesmeyer et al. (1991) documented a tendency for sea surface temperatures to be warmer than normal in the equatorial Pacific since 1976, and these SST anomalies are believed to be the cause of an increased tendency to the strong phase of the PNA circulation pattern beginning in the winter of 1976-77 (Trenberth, 1995). The statistically significant step changes in snowfall, April 1 snowpack and summer flow in Capilano River are consistent with this shift in circulation patterns. However, the climatic significance of these shifts must be considered within a longer time frame. For example, in Fig. 2, the NP index appears to exhibit a shift in the 1940s from dominantly negative values to dominantly positive values, in addition to the shift following 1976. Karl (1988) demonstrated that similar types of decadal-scale climatic fluctuations may not reflect a climatic "change," but could result from a stationary process with low-order autocorrelation caused by some "physically-based weak year-to-year persistence." On the other hand, Trenberth (1995) hypothesised that the anomalously warm tropical Pacific SSTs beginning in the late 1970s may be one of the first manifestations of global warming due to increased concentrations of greenhouse gases, and that the strong phase of the PNA pattern may occur more

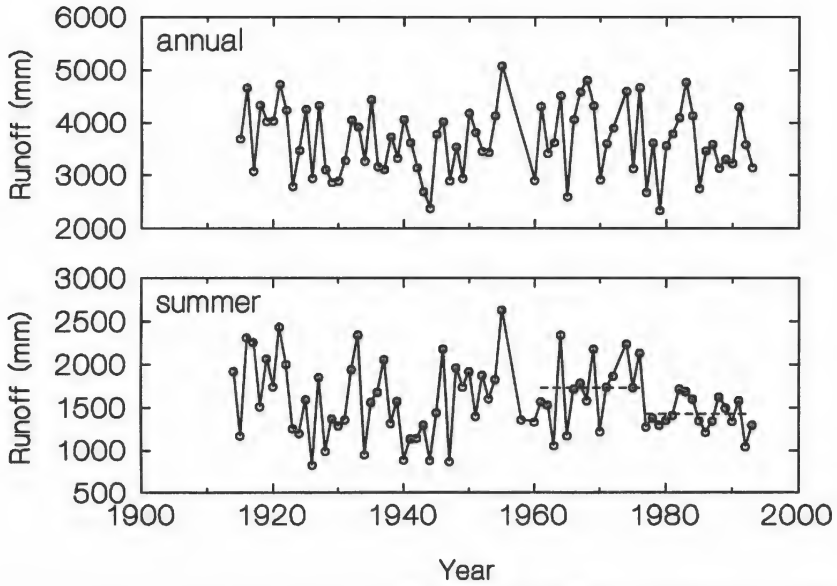

Figure 9. Time series of annual and summer runoff, Capilano River. The horizontal lines in the plot for summer runoff indicate the 1961-76 and 1977-92 means.

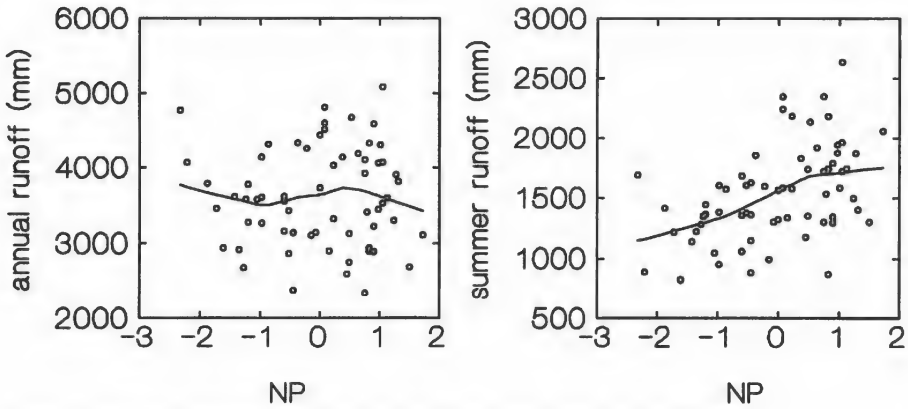

Figure 10. Relations between annual and summer runoff for Capilano River and the NP index.

frequently than in the past. Palmer (1993) similarly hypothesised that climatic responses to global-scale forcing are likely to be manifested in changes in the frequencies of the dominant modes of atmospheric circulation, rather than in the emergence of new modes. If these hypotheses are correct, further examination of past climatic variability and environmental responses in relation to atmospheric circulation may provide insight into the effects of future climatic change.

Conclusions

Winter temperatures in the south Coast Mountain region are correlated with the strength of the PNA circulation pattern as a result of warm, southerly airflow during enhanced-PNA winters. Winter precipitation is not clearly correlated with the strength of the PNA circulation pattern. However, winters with an enhanced PNA pattern tend to experience more rain and less snowfall, resulting

in decreased April 1 snowpack water equivalent even in wet years.

Streamflow response depends on elevation and glacier cover. For a low-elevation catchment with minimal seasonal snow storage, there is no relation between the strength of the PNA pattern and either annual or summer runoff. For a mountainous, unglacierized catchment, there is no relation between PNA strength and annual flow, but there tends to be less summer flow following enhanced-PNA winters because of the decreased spring snowpack. In a glacierized catchment, glacier melt confounds relations between runoff and climate.

Following 1976, there was a statistically significant decrease in snowfall, April 1 snowpack and summer runoff from an unglacierized, mountainous catchment. These decreases are consistent with the post-1976 shift toward the strong phase of the PNA pattern during winter that has been documented in the literature.

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Population Ecology of the Gray-Tailed Vole, *Microtus canicaudus*

Abstract

Voles of the genus *Microtus* play a major role as primary consumers of vegetation and as a prey base for many predators in grassland communities throughout the world. We present demographic and reproductive data from a 2-yr field study of the gray-tailed vole, *Microtus canicaudus*, a little-known microtine species endemic to the Willamette Valley of western Oregon, U.S.A. Population data were recorded on two live-trapping grids from October 1991 through September 1993. Population densities peaked between 1 June and 20 July 1992 at 54 voles/ha. Peak breeding with approximately 80% of adult females pregnant or lactating occurred between May and June with lesser activity in November and December. Very little breeding occurred during late summer and mid-winter months. Recruitment rate averaged 1.6 voles/litter/adult female. Mean home range sizes were twice as large for males (253 m^2) as they were for females (135 m^2). We compare the results from this field study with those obtained from enclosed populations of *Microtus canicaudus* and with those of "cycling" *Microtus* species. We suggest that agricultural practices, fragmentation of habitat, seasonal flooding of grasslands, and predation work in consort to regulate vole population numbers throughout the Willamette Valley of Oregon.

Introduction

Voles of the genus *Microtus* have been studied extensively with respect to their demography, behavior, and general ecology (Tamarin 1985). These voles occur in a variety of grassland habitats, are primary consumers of green vegetation, and are a prey source for numerous predators. Seventeen species of *Microtus* have been recognized in North America (Jones et al. 1992), eight of which have been well-studied. Although interspecific variation occurs among species, the general characteristics of *Microtus* species are that they have high reproductive potential (Keller 1985), exhibit marked population fluctuations often leading to annual or multi-annual (3-5 yr) cycles (Krebs and Myers 1974, Taitt and Krebs 1985, Batzli 1992), utilize a variety of breeding systems typified by polygynous or promiscuous mating (Wolff 1985, Tamarin et al. 1990) and female territoriality (Ostfeld 1985, Wolff 1985), and have male-biased juvenile dispersal (Boonstra et al. 1987, Wolff 1993, Lambin 1994). Voles are used as ecological model species (Ims and Stenseth 1989) to test hypotheses and construct conceptual and mathematical models addressing questions in population regulation (Hanski and Korpimaki 1995, Krebs 1996), behavioral systems (Tamarin et al. 1990), and ecological problems such as habitat fragmentation (Ims et al. 1993). Information on additional species contributes to this data base for comparative analyses addressing related questions in population ecology. We present population data from a 2-yr live-trapping study of the little-studied gray-tailed vole, *Microtus canicaudus*. Specifically we ask if gray-tailed voles possess demographic characteristics associated with rapid population growth and resultant high densities typical of cycling *Microtus* species. In multi-annual cycling voles, densities frequently fluctuate from <5 to >200 voles/ha over a 3-5 yr period (Taitt and Krebs 1985). We also compare the demography of field populations of gray-tailed voles with that of enclosed populations (Manning et al. 1995, Edge et al. 1996, Wolff et al. in press).

Gray-tailed voles are a grass-eating *Microtus* occupying the grasslands of the Willamette Valley of western Oregon and southern Washington (Verts and Carraway 1987). Other than a brief description of the habits and general biology of gray-tailed voles (Verts and Carraway 1987), and laboratory studies on sibling recognition (Boyd and Blaustein 1985), copulatory behavior (Dewsbury and Hartung 1982), and reproduction (McDonald and Forslund 1978, Hagen and

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Forslund 1979), little is known about the ecology of this species. In one open field, enclosure, and laboratory study, Wolff et al. (1994) found that breeding occurred from March through November with a breeding lull in late summer and mid-winter, adult body size ranged from 30-50 g, mean litter size was 4.4, the mating system was polygynous or promiscuous, home ranges of males were twice as large as those of females, and juvenile dispersal was male-biased.

Study Area and Methods

Gray-tailed voles were live-trapped on two 0.5 ha open trap grids at the E. E. Wilson Wildlife Area, 15 km north of Corvallis, in the central Willamette Valley, Oregon (44° 38' N, 123° 12' W). These grids were situated in open grassland habitat dominated by dense growth of perennial grasses, *Festuca arundinacea, Holcus lanatus*, and *Agrostis tenuis*. Each grid consisted of 100 traps in a 10 x 10 array with 7.6 m between stations. One Sherman large-size live trap was placed within 1 m of each station with the front door of the trap intersecting an active vole runway. The two grids were separated by 20 m of untrapped habitat.

Trapping was conducted at 2-wk intervals from 7 October 1991 through 16 September 1993. During a trap week, traps were baited with oats, set each evening and examined the following morning for four consecutive nights. Traps were propped open and pre-baited once during non-trapping days. All captured voles were ear-tagged for identification, and body mass, sex, reproductive condition, and trap location were recorded at each capture. Females were considered in reproductive condition if they were obviously pregnant, lactating, or had widely parted pubic symphyses. Voles were considered adult if they were ≥30 g (Wolff et al. 1994). Testes of mature gray-tailed voles are relatively small (~ 8 mm long; Wolff et al. 1994) and often retracted abdominally and not detectable externally in adult animals. Recruits were defined as any newly marked, <30 g animals caught after the initial population was marked.

Population sizes were estimated using the program CAPTURE and the jack-knife estimator (Rextad and Burnham 1992). Trappability was the percent of marked animals caught each trap week. Population growth rate was estimated by dividing the change in ln(density + 1) between successive trap periods by the number of weeks between trap periods. Mean longevity (not accounting for dispersal) was estimated by subtracting the first from the last week of capture for animals first caught when they weighed <30 g. The ratio of recruits to adult reproductive females was computed by dividing the number of recruits captured each month by the number of reproductive females captured 4 wks earlier. This 4-wk period provided time for juveniles to be weaned, suffer mortality, and be recruited into the population.

Home range area was estimated using the minimum area polygon method (Hayne 1949) for adults that were caught 7-9 times over a 4-6-wk period. Home ranges were not calculated for animals with more than one capture in perimeter traps. Animals caught in perimeter traps often have home ranges that extend beyond the grid and therefore home range sizes would have been underestimated.

From 3 April to 18 May 1995, we trapped and removed voles for 46 consecutive days in one 0.5 ha pen enclosed on the sides and top with chicken wire. This pen excluded all avian and larger terrestrial predators, but allowed for movement of voles. The enclosed pen was located adjacent to our two open-field live-trapping grids. We used these data to get a population estimate of a high density population in the absence of predators.

Results

During the 2-yr study, 579 gray-tailed voles were trapped 3,117 times on the two grids. In addition, 60 Townsend's voles (*Microtus townsendii*), 55 deer mice (*Peromyscus maniculatus*), 87 wild house mice (*Mus musculus*), and 109 vagrant shrews (*Sorex vagrans*) were captured. Only the results from gray-tailed voles are presented in this paper.

Only eight voles (1.4 % of the population) moved between the two grids during the 2 yrs so we treated the grids as independent samples and present the data as means and standard errors of the two grids with an n = 2. The sex ratio did not differ from 1 on either grid (M:F, 166:151 and 125:130, both X^2 <0.18, P > 0.50; sex of seven animals was not determined). Mean trappability (Krebs and Boonstra 1984) over the two years of the study was 84% (se = 0.32%) for males and 74% (se = 0.21%) for females.

Mean population size of voles ranged from 5 to 27 voles/0.5 ha during the 2-yr study (Fig. 1).

Population densities were highest in December 1991, June 1992, and January 1993. The population remained relatively low throughout the remainder of 1993 even during the spring breeding season. The mean weekly population growth rate from April through August 1992 and 1993 was -0.11 (se = 0.283) and 0.00 (se = 0.200), respectively.

Some adult females were in reproductive condition every month except for January 1992 (Fig. 2). Peak breeding activity for females occurred during May-June, with a secondary peak in October. Breeding activity declined considerably in February-March and August-September of both years. Peaks in recruitment followed peaks in female reproductive activity in autumn 1991, summer 1992 and autumn 1992, although relatively low recruitment followed a major peak of female reproductive activity in the summer of 1993. Mean juvenile recruitment/reproductive female was 1.6 (se = 0.25). Fifty-four percent of the animals caught were caught just once. Mean minimum longevity differed significantly between males (3.9 wks, n = 96, se = 0.50) and females (5.8 wks, n = 128, se = 0.65; F = 4.45, P < 0.05).

Due to small sample sizes on each grid, mean home range sizes were estimated for the two grids combined. Mean home range size for males (253 m^2, sd = 138, n = 11) was significantly larger than it was for females (135 m^2, sd = 82, n = 26; $F_{1,35}$ = 9.689, P = 0.004).

During the 46-day trap period in the 0.5 ha predator-exclusion pen in 1995, we caught 308 gray-tailed voles. Very little sign of vole activity was seen outside the pen even though suitable habitat was plentiful. We did not trap the grids during this time, but we saw fewer runways, holes, grass clipping and scat piles than at any time during the 2 yrs of trapping.

Discussion

During the 2-yr field study, population density of gray-tailed voles fluctuated between 5 and 27

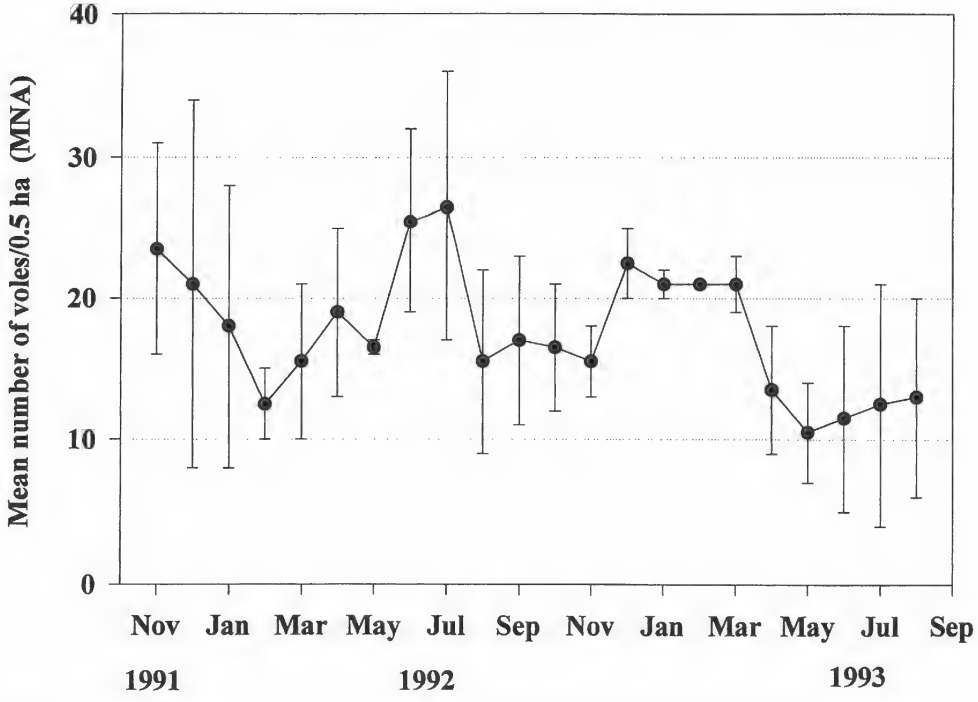

Figure 1. Mean (se) number of gray-tailed voles/0.5 ha from November 1991 to September 1993 at the E. E. Wilson Wildlife Area research site.

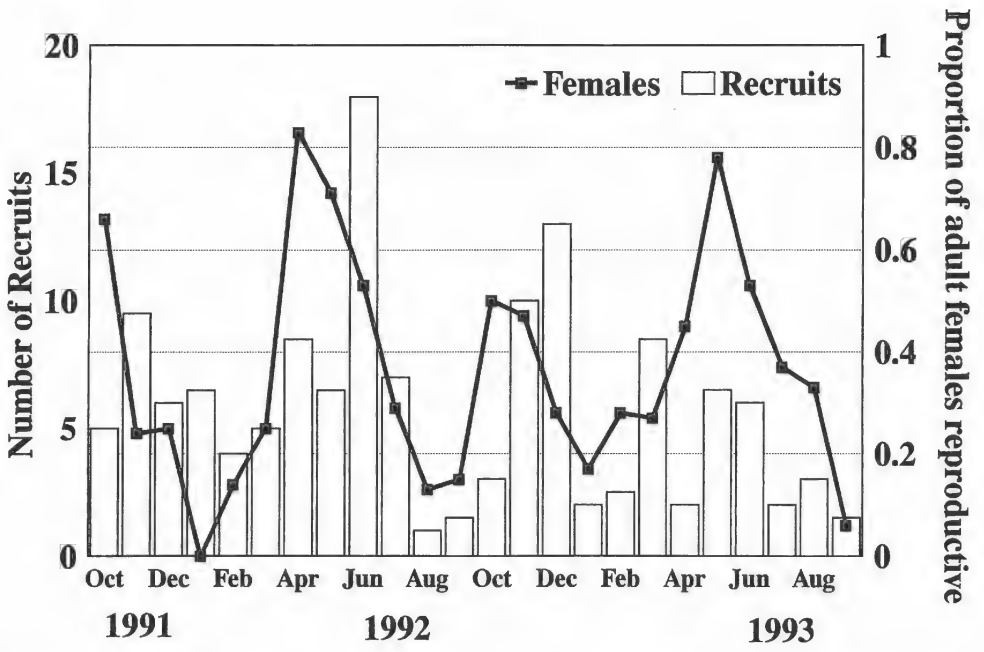

Figure 2. The proportion of adult females that were in reproductive condition and the number of recruits entering the population from October 1991 to September 1993 at the E. E. Wilson Wildlife Area research site.

voles/0.5 ha with no indication of annual or multi-annual cycles. Vole populations that exhibit multi-annual cycles have very distinct changes in density, age ratios, survival, and recruitment from year to year (Krebs and Myers 1974, Taitt and Krebs 1985). We saw none of these characteristics in our population that would indicate a multi-annual cycle was occurring. Reproduction and juvenile recruitment occurred primarily from March-November with a breeding lull in late summer and again in mid winter. This breeding pattern is typical of other microtine rodents at this latitude (Keller 1985). Mean minimum longevity (including survival and emigration) was 3.9 wks for males and 5.8 wks for females and 54% of the animals were caught only once suggesting that animals did not remain long on the study area. With short longevity, an unproductive winter period of 3 months with little recruitment, a subsequent low spring population, and a mean population growth rate during the breeding season near zero or negative, populations did not grow to peak cyclic levels.

The relatively low numbers of voles and lack of evidence for cycling may be related to three interrelated factors: patchy habitats, predation, and seasonal flooding of habitats. The Willamette Valley consists of a mosaic of habitats characterized by agricultural fields and urban environments with <1% permanent grassland (Oregon GAP Analysis Program, F. Faure, personal communication). Also, much of the Willamette Valley is flooded from December through March when an average of 58 cm of rain falls. During this time, many voles are forced out of some areas and confined to others. Throughout the year, but especially during winter, the Willamette Valley hosts a large resident and migratory population of raptors, primarily red-tailed hawks (*Buteo jamaicensis*) and kestrels (*Falco sparverius*), as well as several other species of hawks and owls. The E. E. Wilson Wildlife Area provides refuge for a very dense population of raptors as well as red foxes (*Vulpes vulpes*), coyotes (*Canis latrans*), long-tailed weasels (*Mustela frenata*), and several species of large snakes, all of which have been sighted on the study area. Foraging on voles by great-blue herons (*Ardea herodias*) on the edge of flooded fields is a common sight in the Willamette Valley during winter (personal observations). Patchy habitats and the presence

of diverse facultative predators that consume animals dispersing from patches have been used to explain the lack of cycles for some other microtine populations (e.g. Hansson and Henttonen 1985, Hanski et al. 1991, Korpimaki and Norrdahl 1991).

Our census of voles in the predator-exclusion pen in spring 1995 demonstrates that gray-tailed voles have the potential to reach high densities that could lead to cycles. We caught 308 voles in a 0.5 ha pen that were designed to exclude all avian and large terrestrial predators. The number of voles caught likely represents the number of voles in the pen rather than immigrants during the 46-day removal period because very little sign of vole activity was seen outside the pens. On our trapping grids adjacent to these pens, we also saw very little sign of active runways, burrows, clippings, or scat piles. These results suggest that in the absence of predators, gray-tailed voles were able to achieve extremely high densities (616 voles/ha), similar to peak densities in cycling *Microtus* species (Krebs and Myers 1974, Hansson and Henttonen 1985, and others).

Very little historical information is available regarding the relative abundance of gray-tailed voles, but in November 1974, voles were reported to be "numerous" and at "peak" or "cyclic" densities near our study site (B. J. Verts, personal communication). Also, Goertz (1964) reported that gray-tailed voles exhibited episodic irruptions, but not with a predictable frequency. It appears that gray-tailed voles have the potential to reach higher densities than those measured on our open grids, but we suggest they may be prevented from reaching this potential by heavy predation and existence in a patchy and fragmented landscape.

For the last 3 yrs, our research group has conducted experiments with gray-tailed voles in 0.2 ha enclosures that have been planted with alfalfa (*Medicago sativa*; Manning et al. 1995, Edge et al. 1995, in press, Schauber et al. in press, Wolff et al. in litt.). We present some comparisons of the demography and behavior of voles in the two study sites. All analyses were conducted using the same methods. Population densities in the enclosures frequently reached an equivalent of 350 to 500 voles/ha (Edge et al. in press, Schauber et al. in press) and >2,000 voles/ha in habitat fragmentation studies (Wolff et al. in litt.) which is considerably higher than the 54 voles/ha recorded from our field site. The proportion of females in the population that were in reproductive condition during the breeding season averaged about 80% at both sites and juvenile recruitment rates were comparable at about 1.6 juveniles/adult female (Edge et al. in press, Schauber et al. in press). Minimum longevity of voles was greater in the enclosures than on the open grids for both males and females (Table 1). However, longevity of voles on open grids is confounded by emigration, so is not directly comparable to longevity in the enclosed populations where emigration was not possible. Mean weekly population growth rates throughout the spring and summer on open grids was -0.11 in 1992 and zero in 1993 (mean -.054 for the two years) compared to 0.09 and 0.14, respectively, in the enclosed grids (mean of 0.11) and 54% of the voles were caught only once on

TABLE 1. Comparison of demographic features of gray-tailed voles on the open grids at the field site and enclosed grids at Hyslop Farm; mean (se). Data from enclosed grids are from Edge et al. (in press) and Schauber et al. (in press).

	Open grids	Enclosed grids	P
Maximum density, voles/ha	54	350-500	
Animals caught only once	54%	24%	
Population growth/week*	-0.054 (0.229)	0.11 (0.028)	Mann-Whitney$_{1,14}$, P = 0.093
Longevity, wks			
males	3.9 (1.24)	6.4 (0.62)	$F_{1,8} = 3.141$, P = 0.114
females	5.9 (1.38)	8.7 (0.69)	$F_{1,8} = 3.315$, P = 0.106
Home range size, m^2			
males	253	93	$F_{1,44} = 31.7$, P < 0.001
females	135	56	$F_{1,48} = 17.3$, P < 0.001

*mean population growth/week during the May-August breeding season for the two years combined.

open grids compared to 24% in the enclosures (Table 1; Edge et al. in press, Schauber et al. in press). Growth rates near or below zero and higher mortality (and/or dispersal of animals off the open grids) could have kept the open populations at relatively low numbers. The relatively high population growth rates and lack of dispersal in the enclosed population may all have contributed to the high densities (Krebs et al. 1969, Boonstra and Krebs 1977, Ostfeld 1994). Our two sites consisted of different vegetation (alfalfa in enclosed habitat and mixed pasture grasses in the open habitat) however voles apparently do equally well in both habitats and may even prefer grasses (e.g. *Microtus ochrogaster* and *M. pennsylvanicus*, L. Getz, pers. comm.). The fact that densities in the enclosed populations often reached >350 voles/ha compared to a maximum of 54 voles/ha in the field suggests that any intrinsic or self-regulating mechanisms were not effective in limiting population growth in the enclosures (Wolff and Schauber 1996, see also Heske and Bondrup-Nielsen 1990).

At both sites, home ranges of males were twice as large as those of females, but home ranges at the field site were twice as large as they were in enclosures for both sexes (Wolff et al. 1994; Table 1). Home range size in small mammals is quite flexible and subject to variations in habitat quality and population density (Ostfeld 1985, Wolff 1985, Boutin 1990). In one experiment in our enclosures, densities approached 3,000 voles/ha and we recorded home range sizes of ~25 m^2 with as many as 9-12 voles sharing a home range (Wolff and Schauber 1996).

We conclude that gray-tailed voles possess attributes common of other *Microtus* species. The high reproductive potential can lead to high densities, however, population size and/or multi-annual cycles seem to be limited by extrinsic constraints. Gray-tailed voles are flexible in their behavior and social structure as evidenced by the comparisons of home range size and overlap in open and confined populations. We suggest that habitat fragmentation in conjunction with winter flooding that further limits habitat occupancy increases vulnerability of voles to predators which prevents populations from reaching cyclic densities. Occasional population irruptions potentially can occur under an appropriate set of extrinsic conditions.

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Ten-year Diameter and Basal Area Growth of Trees Surrounding Small Group Selection Openings

Abstract

The effects of small openings in forest stands has interested silviculturists and ecologists for years. Interest generally has centered on the vegetation in the openings, not on that immediately outside of them. Quantitative information on the growth of trees adjacent to group-selection openings, although often mentioned in forestry textbooks as contributing to cost effectiveness, is scant. Five conifer and three hardwood species bordering 9-, 18-, and 27-m diameter openings in the northern Sierra Nevada of California were examined for diameter growth 10 years before and 10 years after an initial group selection cutting. Ten-year diameter growth at breast height of various combinations of species and diameter classes did not differ significantly ($P > 0.05$) among opening sizes 10 years after cutting. But mean basal area growth of pines (ponderosa and sugar) 10 years after cutting was significantly greater ($P < 0.05$) than that before cutting in 18- and 27-m openings. This difference also was found for shade-tolerant conifers (Douglas-fir, incense-cedar, and California white fir) bordering all opening sizes. Mean basal area growth of hardwoods (California black oak, tanoak, Pacific madrone) did not differ before and after cutting for any opening size.

Introduction

Today, as never before, sentiment is shifting toward forest management systems that are perceived as being more gentle on the land, its vegetation, and its creatures. Sustaining ecosystems and not chronically disrupting ecosystem processes are the watchwords of modern forestry. Smith (1962) noted that "The group selection method is more readily adapted to a wide variety of conditions than any other because the ecological requirements of most species can be met within its framework." Furthermore, the small, scattered openings created by timber harvest suggest small-scale natural disturbances such as those created by small hot fires.

The group-selection cutting method, which is part of an uneven-aged silvicultural regeneration system, involves the removal of groups of trees to create small openings that range from 0.01 to 0.8 ha. The upper size limit of openings is governed primarily by the environment in them. Openings should not be so large as to lose the site protection of the surrounding trees (Daniel et al. 1979). Thus, slope, aspect, and height of surrounding trees influence opening size. Several openings, scattered throughout a stand, usually are harvested together on a cyclical basis. The cycle often is 10 to 20 years. There is no rotation and cutting continues in perpetuity, usually removing clusters of mature trees. Initial and early entries into the stand, however, usually have an element of "improvement" in them, whereby trees of younger ages are removed. Indeed, the necessity for cutting small trees "is felt especially in making a first cutting in previously unmanaged stands" (Hawley 1946). This gives opportunity to lower the proportion of less desirable species, trees with poor growth, those that interfere with the growth of better trees, and poorly formed, slow-growing, and diseased individuals.

Increased growth of residual trees after cutting is generally considered to be beneficial. But for group selection, the growth of trees surrounding the openings is seldom quantified and its amount has not been reported for mixed conifer and hardwood species in the western United States. The minimum opening size required to influence tree growth and the distance into the stand beyond which the openings will have little or no effect are equally unreported. This paper presents results on these subjects from a study that quantified 10-year diameter and basal area growth of various sizes and species of trees before and after group-selection cutting in three sizes of small openings.

Methods

Site and Species

The study was located on the Challenge Experimental Forest in north central California. Here, site quality is high and the dominant species,

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ponderosa pine (*Pinus ponderosa* Dougl. ex Laws. var. *ponderosa*), will average 34 m in height in 50 years (Powers and Oliver 1978). Summers on the Experimental Forest are hot and dry; winters cool and moist. The average midsummer maximum temperature, based on 43 years of record, is 32 °C; the midwinter minimum is -1 °C. The growing season is about 200 days. Precipitation averages 1727 mm with 94 percent falling between October and May. Moisture is the limiting factor for growth, and drought often predisposes less vigorous trees to attack by insects and disease. Aspects are mostly northeast and southwest and slopes vary from 3 to 30 percent. Texture of the soils is clay loam grading with depth to clay. Soils tend to be deep, moderately well drained, and quite fertile.

In addition to ponderosa pine, other tree species on the Forest are Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), sugar pine (*Pinus lambertiana* Dougl.), California white fir (*Abies concolor* var. *lowiana* [Gord.] Lemm.), and incense-cedar (*Libocedrus decurrens* Torr.) (Little 1979). Hardwoods, principally California black oak (*Quercus kelloggii* Newb.), tanoak (*Lithocarpus densiflorus* [Hook. & Arn.] Rehd.), and Pacific madrone (*Arbutus menziesii* Pursh) are scattered throughout as individual trees, clumps, or groves. The Forest consists of a broad mosaic of even-aged stands resulting from past logging and fires. The oldest dominant and codominant conifers in the study area were about 100 years old when the study began and averaged about 77 per ha, 70 percent of which were ponderosa pines. Typical of stands in the northern Sierra Nevada, a few overmature hardwoods were present along with a large component of younger trees of shade-tolerant species (Douglas-fir, California white fir, incense-cedar, and tanoak) (Rundel et al. 1977). Altogether, trees larger than 8.9 cm in diameter at breast height (d.b.h.) numbered 613 per ha and contained about 62 m^2 per ha of basal area.

Location and Environment

Groups of large and small trees, which were located in two units located within 1.5 km of each other on relatively homogeneous ground having similar soil and growth potential, were logged in the fall of 1963 to form circular openings of about 9, 18, and 27 m in diameter (crown dripline to crown dripline). There were 27 openings in one unit and 21 in the other. The smallest size opening was created by removal of several medium- to small-sized trees; the largest by removal of several large, medium, and small trees. Surrounding trees were of all sizes. Each opening size was replicated 16 times. Location of openings was random with the restriction that they be within 60 m of skid roads. In May 1964 unmerchantable conifers and hardwoods were removed and the ground scarified by a bulldozer. As a result, each opening was free of vegetation, at least above ground. Below ground, roots of border trees probably had room to expand into area formerly occupied by cut trees.

Measurements and Analysis

In spring 1964, shortly after harvest, trees surrounding the 48 group-selection openings were visually evaluated to determine the distance from the opening edge where they no longer received additional light from the opening or where their roots most likely would not be able to extend into it. Altogether, 677 conifer and hardwood trees in the breast-height diameter range of 10 to 106 cm comprised the after-logging sample (Table 1). No trees beyond 6 m were judged to be affected by creation of the openings. All trees were remeasured in August 1973 or after 10 complete growing seasons.

The before-logging sample was done retrospectively by boring trees at breast height and calculating radial growth from 1954-1963, which was doubled to arrive at diameter growth. Because the prelogging measurements were inside bark and the after-logging measurements were outside bark, they needed to be reconciled. Specifically, the after-logging data needed to be corrected for bark growth during the 10-year period. This task was accomplished by using the corrections formulated by Dolph (1981) for the five conifer species. No corrections were available for the hardwood species.

For the before-logging sample, we randomly chose one of the two units. It had 27 openings in it, 9 of each size. To check the previously determined opening-influence limit of 6 m, we measured additional trees 6 to 13 m from the opening. Altogether, 372 trees, located 0.5 to 13 m from the opening edge comprised the prelogging sample (Table 1). The distance of each tree from the opening edge was recorded.

TABLE 1. Number of sample trees bordering openings after logging (48 openings) and in prelogging (27 openings) period by diameter, class and species.

Diameter class (cm)	Species	After logging opening diameter (m) 9	18	27	Before logging
		No. of trees			
10 to 30	Ponderosa pine	4	7	5	15
	Sugar pine	—	1	1	1
	Douglas-fir	24	28	30	52
	Calif. white fir	1	7	4	3
	Incense-cedar	24	34	43	68
	Hardwoods	18	11	33	14
31 to 60	Ponderosa pine	35	53	46	86
	Sugar pine	1	—	1	—
	Douglas-fir	14	23	22	38
	Calif. white fir	—	1	3	2
	Incense-cedar	13	11	12	24
	Hardwoods	5	2	5	3
>61	Ponderosa pine	32	35	61	53
	Sugar pine	4	—	2	—
	Douglas-fir	5	5	7	11
	Calif. white fir	—	—	—	—
	Incense-cedar	—	—	—	—
	Hardwoods	2	—	2	2

To determine tree growth and distance relationships, data were analyzed by regression and the analysis of variance (ANOVA) therefrom, and paired t tests (Wilkinson 1989). Statistical significance in all tests was at $\alpha = 0.05$. Both d.b.h. and basal area were considered to evaluate growth, and many transformations of both were examined for normal distribution of residuals, constancy of variance, and trend of residuals relative to predicted values. The model in this paper best met the assumptions of normality and provided the best fit.

Steps in the analysis were first to determine the distance into the adjacent stand where trees were influenced by the openings. The next step was to analyze for possible differences in before- and after-logging stand growth. The third step was to examine the after-logging data to determine possible differences in 10-year diameter growth among species and tree size classes for the different opening sizes. Because the first analysis indicated no significant effect beyond 6 m, we used data from the 48 openings in the after-logging analysis.

Results

Tree Growth and Distance from Opening Edge

We found the best expression to document the influence of the openings to be a linear equation of the difference in 10-year basal area growth before and after logging. Based on this difference, little growth occurred on trees farther than 6 m into the forest (Figure 1). The equation was of the form:

$$Y = \beta_1 + \alpha_1 D + \alpha_2 \ln(D) + \varepsilon$$

in which:
$Y = dba_1 - dba_0$
D = distance from opening edge (m)
dba_0 = inside bark basal area growth for 10-year period before harvest (cm^2)
dba_1 = inside bark basal area growth for 10-year period after harvest (cm^2)
β = intercept term for the ith opening size
α = coefficients, and
ε = random error.

We found a weak relationship between the difference in before- and after-logging basal area growth and distance from opening edge. The highest r-squared values, which were for trees adjacent to the largest opening size, were 0.11 for pines, and 0.06 for tolerant conifers. Both values were significant at $P = 0.05$, but are of no practical significance. Although the difference in growth for the 10-year period tended to decrease as distance from the opening increased (Figure 2), we were unable to objectively define a specific distance from the opening edge where the opening ceased to have an influence. An exception to the decreasing growth trend was that some trees on

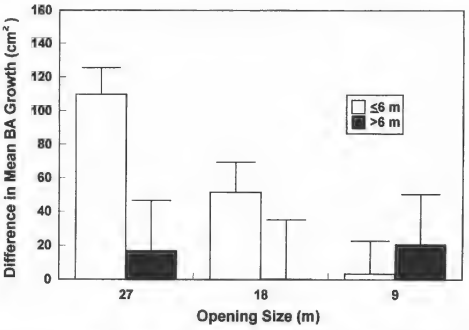

Figure 1. The difference in mean before- and after-logging inside bark basal area (with standard errors) suggests that little growth accrues to trees farther than 6 m into the forest, at least for 18- and 27-m diameter openings.

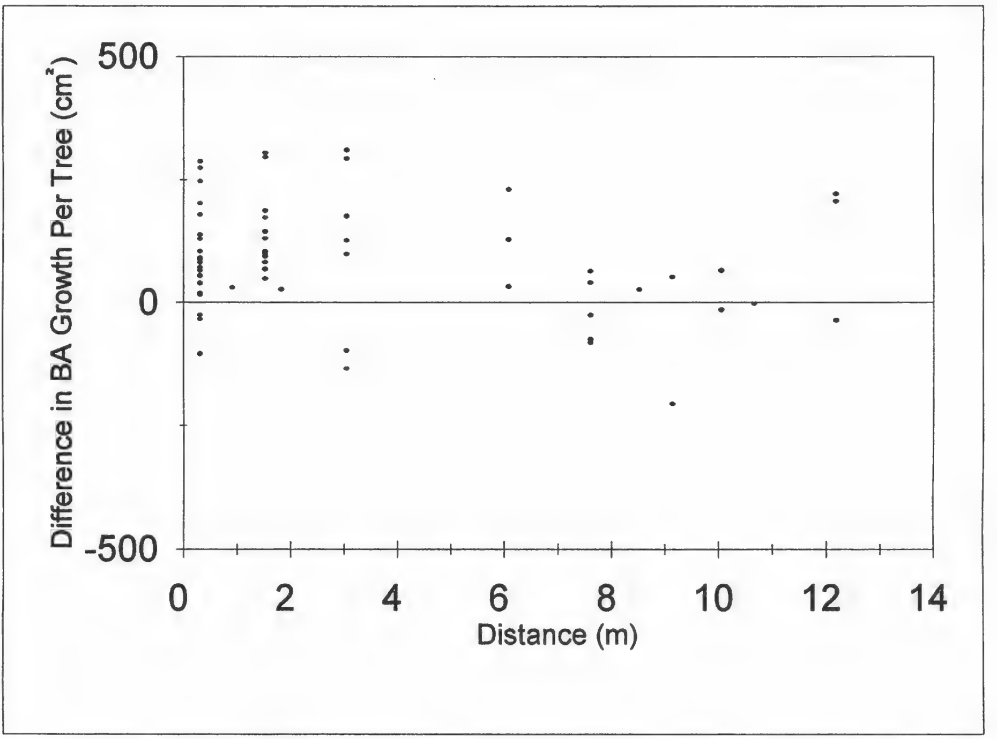

Figure 2. Example of the difference in before- and after-logging 10-year basal area growth per tree relative to distance from opening for pines in 27-m openings, Challenge Experimental Forest, north central California, 1973.

the edge of openings appeared to grow less than those farther back in the forest (Figure 2). This difference may be the result of shock caused by opening up the stand or possible damage to roots from logging.

Before and After Logging Comparison

Mean 10-year basal area growth after logging differed significantly from mean 10-year basal area growth before logging for pines bordering 18- and 27-m diameter openings, and for shade-tolerant conifers adjacent to 9-m, 18-m, and 27-m diameter openings (Table 2). The difference in 10-year basal area growth of hardwoods before and after logging did not differ significantly among opening sizes. And in one instance (27-m diameter openings), hardwoods actually grew 52 percent slower. We believe, however, that this negative response has little practical importance and no statistical significance ($P = 0.23$).

For those species and opening sizes where growth increased after logging, the basal area growth increase ranged from 9 percent for pines adjacent to 18-m openings and for tolerant conifers next to 9-m opening to 87 percent for hardwoods adjacent to 18-m diameter openings (Table 2). When all species and opening sizes were combined, the average net 10-year basal area growth increase resulting from logging was 24 percent.

Diameter Growth and Opening Size

Average 10-year diameter and basal area growth after logging were examined statistically to determine which variable explained the most variation. Based on ANOVA, no statistically significant differences in breast-height diameter were found among species or diameter classes among opening sizes (Table 3). Overall (but not significant) trends in mean values were: diameter growth was greater for large trees than small trees; growth

TABLE 2. Average 10-year basal area growth of trees in group selection openings by species class and size of opening before and after logging.

Species class	Opening diameter (m)	Before logging (cm^2/10 yrs)	After logging (cm^2/10 yrs)	Increase (decrease) (pct)	Standard error of difference (cm^2)	P[α]
Pines	9	436	439	0	17	0.43
	18	370	405	9	18	0.05
	27	408	516	26	20	0.01
Tolerant conifers	9	215	234	9	10	0.04
	18	191	226	18	6	0.01
	27	160	224	40	14	0.01
Hardwoods	9	53	83	57	12	0.06
	18	60	112	87	23	0.07
	27	279	183	(52)	120	0.23
Average				24		

[a]Tail probability (P-value) of the paired t-statistic between the before and after logging values on each line. P values < 0.05 are considered significant for individual tests. If simultaneous tests for the three openings are desired, then P < 0.05/3 = 0.016 are considered significant (Bonferroni t-test).

TABLE 3. Average ten-year diameter growth of various combinations of tree species and sizes bordering group selection openings, 1964-1973.

Species combination	Diameter class (cm)	Opening diameter (m)	Diameter growth (cm/10 yrs)	Increase (pct)	Root mean square error (cm)	F	P
Pines	10 to 30	9	2.8[a]	9	2.9	0.34	0.72
		18	2.8	14			
		27	4.1	19			
	31 to 60	9	3.8	8	2.0	2.80	0.07
		18	4.3	8			
		27	5.1	10			
	>61	9	4.8	6	2.0	0.58	0.56
		18	4.8	7			
		27	5.3	7			
Tolerant conifers	10 to 30	9	3.0	16	2.2	0.57	0.57
		18	3.3	16			
		27	3.6	19			
	31 to 60	9	4.6	11	2.1	0.53	0.59
		18	4.8	12			
		27	5.1	12			
	>61	9	5.6	8	2.5	0.69	0.52
		18	7.4	9			
		27	7.4	10			
Hardwoods	10 to 30	9	3.6	21	2.5	0.54	0.59
		18	4.3	28			
		27	4.3	25			
	31 to 60	9	4.6	11	2.3	1.16	0.36
		18	5.8	18			
		27	3.0	6			

[a]No significant differences in diameter growth at the 5-percent level were found among opening sizes for each diameter class and species, based on ANOVA.

was greater for trees adjacent to the largest opening size; and shade-tolerant conifers grew better than less tolerant pines. Hardwoods grew better than conifers in the smallest diameter class.

Discussion and Conclusions

The juxtaposition of trees of many sizes relative to each other and to distance from the edge of small openings is such that the amount of light and soil moisture that each tree gains from new group-selection openings is highly variable. Large trees, well back from the opening, have an advantage over small trees because their large crowns and root mass enable them to exploit the typically small spaces where light filters through and where roots can extend into new openings. And large trees, located near the opening boundary, may deny site resources from the opening to trees behind them. Smaller trees, in general, need to be closer to the openings to gain additional resources from them. Consequently, growth of trees adjacent to openings is influenced by tree size, distance from opening, and position of other trees. Because of this combination of factors, we found it difficult to regress tree growth to distance from opening edges. McCreary and Perry (1983) also found it difficult to regress basal area increment to distance for 35-year-old Douglas-fir trees adjacent to strip thinnings near Corvallis, Oregon.

The adjacent tree root/opening size interaction also is a factor affecting tree response. In a separate study on a nearby area on the Experimental Forest, Ziemer (1968) measured soil moisture around a forest-grown but completely released (all other trees removed) 70-cm diameter sugar pine. He found that "soil moisture depletion extended outward to a distance of slightly over 6 m from the base of the tree and somewhat deeper than 5 m under the tree." Presumably, this zone of depletion was caused by moisture-absorbing tree roots. Consequently, at least some roots of adjacent trees probably were already present throughout the 9-m wide openings. And because only a few trees were removed to create this size of opening, most of the opening already was occupied by tree roots. The combination of already-present roots, little new area free of roots, and probable rapid expansion of existing roots tended to mitigate the response from adjacent trees.

Basal area growth of trees adjacent to 9-m diameter openings, in general, was not any better than that of trees farther back in the stand. But pines and shade-tolerant conifers near 18-m openings grew significantly better. These findings suggest that the minimum opening size required to enhance tree growth lies between 9- and 18-m in diameter.

In this study, we visually surveyed hundreds of trees adjacent to openings and judged that no tree beyond 6 m was influenced by the openings. This finding, Ziemer's work, and our graphical results (Figure 1), indicate that 6 m is about the limit of influence from these small sizes of openings in the conifer and hardwood stands on the Experimental Forest. McCreary and Perry (1983) found that increases in basal area growth of Douglas-fir trees in western Oregon extended 3.1 m into the uncut forest. They also cited a Swedish study with Scotch pine (*Pinus sylvestris)* where diameter growth "greatly increased," but only on trees up to 3.0 m in the unthinned stand. Based on these studies, it appears that the influence of small openings and thinnings on adjacent trees is limited in terms of distance into the uncut stand, but within this affected zone, stem growth of trees is significantly increased. These findings may be of interest to ecologists (Sousa 1984, for example) who have long been intrigued by the effect of gaps in the forest canopy.

In our study, pines and tolerant conifers grew significantly better after logging than before logging in the larger openings. When considering the group selection cutting method, forest managers can now ascribe a modest amount of basal area growth (24 percent in 10 years) to trees bordering small-sized openings on sites typical of this study. This growth, as well as the abundant conifer and hardwood regeneration noted in these openings (McDonald and Abbott 1994), add to the applicability of this cutting method.

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Functional Wetland Restoration: An Ecosystem Approach

Introduction

Functional wetland restoration is the culmination of more than a decade of wetland mitigation activity, which has progressed from scattered wetland creation projects to large-scale restoration efforts integrated with and directed at improving ecosystem function. This paper presents a brief history of wetland mitigation and discusses the evolution of functional wetland restoration in the context of a regulatory framework. This paper also provides descriptions of the tools that have been developed specifically to support the move towards functional restoration, including a hydrogeomorphic wetland classification system (HGM) based on geomorphic setting and hydrologic regime, and an associated functional assessment methodology. The hydrogeomorphic functional assessment methodology currently under development is briefly described along with a discussion of the use of reference sites. The paper concludes with a discussion of additional elements to consider to successfully restore ecosystem function, including the need to include areas beyond the boundaries of jurisdictional wetlands, and the rationale for conducting landscape and ecosystem-level evaluations.

Background

Most regulations governing wetlands protection require compensatory mitigation when impacts to wetlands result in lost acreage or function. Local regulations have often focused mitigation efforts on in-kind (i.e., replacing a forested, scrub-shrub or emergent vegetation community with a similar community) and on-site wetland acreage replacement. Mitigation requirements were often fulfilled by wetland creation projects requiring extensive earthwork and hydrologic controls to deliver and maintain water levels. Efforts to address wetland functions in mitigation design were framed in the context of engineered or constructed wetlands. Functions such as flood storage, detention time, and water quality improvement were selected, and mitigation designs often produced systems that looked like naturalized stormwater detention or water quality treatment ponds. Wetland mitigation projects emphasized a few specific functions which could be easily assessed by measuring basin characteristics such as the size of the wetland, depth of storage, and inlet and outlet conditions. Wetland plant community establishment was often a matter of commercial availability, or even sometimes more a horticultural proposition

reflecting what the site could support rather than a natural assemblage of species.

"No net loss of wetlands" has generally been measured on an acreage basis, with different ratios of mitigation area to impact area established for wetlands rated with systems adopted by regulatory agencies. Wetland rating systems, based on a generalized functional assessment, provide a way of assigning a value to different wetlands based on criteria such as size, vegetative complexity, habitat diversity, and water storage or treatment capabilities. Highly rated wetlands require larger mitigation ratios as compensation for wetland losses. The rationale behind the compensation ratios is that complex systems take more time to develop, therefore a greater number of mitigation acres is required to account for the time lag before the mitigation wetlands can provide the functions lost due to impact. In part, compensation ratios also reflect the degree of certainty we have about our ability to replicate the complexity and functions of highly rated wetlands.

Early mitigation efforts resulted in many unsuccessful projects that contributed little to overall wetland and ecosystem function. Created wetlands often suffered from lack of appropriate hydrology, soils, and plantings, and also lacked connections to large, functioning ecosystems. In addition, the isolation of many early mitigation projects resulted in a piecemeal replacement of wetlands that did little to mitigate the cumulative effects of scattered wetland losses.

Restoration has several advantages over wetland creation because some of the elements of a functioning wetland (for example, soils or hydrology) are already in place, and the restoration site is often part of a larger system. The regulatory requirement for on-site mitigation often resulted in poor mitigation planning because the conditions for restoration were either not available or were less than optimal. Where environmentally preferable, off-site mitigation has became more acceptable due to opportunities for connection to larger, functioning systems, and the greater potential for restoration of wetland function through careful site selection.

Wetland Functional Assessment

At the same time attention was focused on improving the quality of mitigation projects, efforts were underway to develop better methods of assessing wetland functions. The first step towards creating a new functional assessment methodology was to develop a wetland classification system based on physical and landscape characteristics. Research sponsored by the U.S. Army Corps of Engineers resulted in the Hydrogeomorphic (HGM) classification for wetlands (Brinson, 1993), which identifies wetland types based on their geomorphic setting and hydrologic regime. Because the HGM classification identifies wetland types by their position in the landscape as opposed to vegetation cover, HGM provides the opportunity to relate specific categories of wetland function to specific types of wetlands.

In a second phase of research, the HGM functional assessment methodology (Brinson et al. 1994, Smith 1993) focuses on the relationship between wetland functions and the hydrologic and geomorphic controls afforded by the surrounding landscape setting. It uses functional indicators both to represent categories of wetland function, and to describe the characteristics and processes of the different wetland types. Because the HGM wetland classification is landscape-based, an HGM functional assessment has to be developed for each geomorphic region. The goal of an HGM functional assessment is to define the specific categories of wetland function associated with a given wetland type (i.e., not all wetlands perform the same functions), as well as the average and range of values expected for the individual functional indicators. The variability and mean values for indicators of specific wetland function(s) are different for similar wetland types in different regions. Efforts are currently underway to regionalize the application of the HGM assessment in Washington State and in other parts of the country.

The application of the HGM classification system and associated functional assessment methodology in the wetland regulatory framework is twofold. First, as a descriptive tool, wetlands can be described and impacts can be assessed relative to a set of commonly agreed upon functional indicators. Second, as a measurement tool, the adequacy of mitigation for functional losses can be evaluated by measuring differences between the pre- and post-project conditions of both the impact and mitigation sites. In assessing an individual site, either impact or mitigation, a functional profile is constructed using site-specific measurements or estimates of functional indicators

for pertinent functions such as hydrology, water quality, biogeochemistry, plant communities, and fish and wildlife habitat. Measurement of the functional losses or gains due to proposed actions (either impact or mitigation), requires assessing the same functional indicators at a series of reference sites. The reference sites should exhibit the same hydrogeomorphic characteristics as the project site and should reflect a range of conditions from degraded (or early seral) to pristine (or late seral) with several sites in between to construct a functional gradient against which the magnitude of impact or mitigation actions can be measured. Once an appropriate suite of wetland functions has been identified and specific functional indicators have been agreed upon, the use of reference sites allows evaluation of individual sites for the potential functional gain achievable from restoration actions. Conditions in the higher functioning reference sites also guide the development of restoration design criteria and can provide measurable performance standards for individual mitigation actions.

Functional Restoration

Restoration is fundamentally an intervention in the projected recovery rate of a given site. Functional restoration undertakes actions at the individual site level that are integrated with ecosystem function at the landscape level. While HGM has the potential to describe individual wetlands in the context of larger ecosystem processes and functions, at this time additional landscape and ecosystem analysis would be required for this level of assessment. Projecting a positive or negative trend in ecosystem function results in a determination of the natural recovery rate of a site and depends to a large extent on conditions in the surrounding watershed and on expected future conditions based on current and proposed land management practices. Therefore, in addition to the HGM assessment of immediate on-site conditions, developing a functional restoration requires broader landscape and ecosystem levels of analysis.

A landscape-level analysis focuses on the conditions in the landscape surrounding the impact, mitigation, and reference sites, and considers the effect of historic, current, and proposed land management practices on the individual functional indicators. For example, a landscape-level analysis would evaluate the effects of grazing or forest practices on sites with similar characteristics, but with different levels of land management activities in the surrounding landscape. Landscape analysis also results in an evaluation of a site's capacity for recovery given the conditions in the surrounding landscape. The Washington Watershed Assessment Protocol (WAP) is an example of a systematic method for conducting a landscape-level analysis focusing primarily on the physical processes in a basin (Washington Forest Practices Board, 1995). WAP evaluates the condition of a basin by assessing hillslope stability, hydrology, riparian condition, and the combined effects of organic and inorganic inputs on fisheries habitat and stream channel condition. Watershed assessment provides a process-driven assessment of the condition of a basin down to the level of an individual stream reach. In addition to identifying constraints on land management practices, it can be useful in identifying critical preservation and restoration opportunities. Understanding the control that human activities exert on the disturbance regimes of an ecosystem allows projections about expected future conditions.

From an ecosystem perspective, the information from a landscape analysis provides a basis for understanding the processes contributing to the pattern and structure in the landscape. Ecosystem analysis addresses the larger issues of biodiversity, connectivity, large-scale wildlife considerations, and patch dynamics. Ecosystem goals that have been formalized into comprehensive land management plans help prioritize specific ecosystem functions and provide guidance for site selection for restoration. The combination of site-level, landscape, and ecosystem assessments comprises a broad ecosystem approach with direct applicability to functional restoration. Functional restoration results from evaluating interactions between the parts of a basin, and identifying prescriptive actions to protect or restore the integrity of the basin as a whole.

Summary

In addition to providing a metric for wetland function for regulatory purposes, the HGM functional assessment evaluates a broad suite of wetland functions such that specific goals for functional restoration can be established. In addition to HGM, an evaluation of broader landscape and ecosys-

tem-level functions helps locate where the most functional gain can be achieved and maintained. Although regulation is concerned with jurisdictional wetlands, most local ordinances require buffers along streams and wetlands in recognition that ecosystem function extends beyond the immediate wetland boundary to include the adjacent uplands. In planning functional restoration projects it is important to consider the interactions between upland and wetland areas, and work within the bounds of functional geomorphic units such as floodplains or riparian zones, rather than restrict our actions only to jurisdictionally-recognized areas.

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Northwest Science Forum

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"Science" in *Northwest Science*: Changes in Journal Content Over the Past 70 Years and What It Tells Us

Introduction

The Northwest Scientific Association (NWSA) was founded in 1923 in Spokane, Washington by academic teachers and scientists primarily from colleges and universities in the inland Northwest. The mission of the association was to "promote scientific research and the diffusion of scientific knowledge". These efforts were centered around a yearly meeting held at various locations in the inland Northwest. In 1927 the journal *Northwest Science* (NWS) was begun. The journal was also to provide a forum for the dissemination of scientific information of interest to scientists in the region as well as a method to communicate events of interest to scientists and teachers in the region. An important component of the journal was to document the discussions and papers given at the annual meetings, and since the beginning, one issue (or a portion there of) a year has been devoted to abstracts of the oral presentations.

Like most scientific journals, NWS science has undergone several format changes over the years. However, most of the alterations have been largely cosmetic, involving changes in the format of the cover. Between 1944 and 1959 the cover depicted a beaker and flask reflecting an orientation toward the laboratory sciences that was reflected in the journal content as illustrated in Table 2. Contents of the journal were first put on the cover in 1944. In 1959 the cover changed to one containing a map of the Northwest, a characteristic retained in the most recent change which streamlined the cover in 1995.

From its inception, the editors of NWS encouraged the submission of and received articles from a wide range of disciplines. The purpose of this paper is to illustrate the scope of the subject matter published in the journal, and to reflect on what this reveals about the direction in which NWSA is heading. In doing so, I hope it stimulates members of the society to rethink or reaffirm the mission of the society.

Methods

The data for this article were compiled by placing all citations from issues of NWS from 1927 through May 1996 in the commercial bibliographic computer software Pro-Cite. Each article was assigned relatively broad keyword(s), reflecting subject content as interpreted by this author. These keywords and terms in the article title were used in the subsequent searches. It is recognized that there is some inherent subjectivity in the terms used. However, the author has had extensive experience in directing programs to catalog resource studies in the national parks - compiling to date over 20,000 records. A list of the terms that occurred in at least .01% of the total number of records is given in Table 1.

Results

Between 1927 and May of 1996, 1634 articles appeared in NWS. The abstracts of the papers given at the national meetings were not included in this analysis. As shown in Table 1, these articles covered a broad range of subjects. To analyze the changes in journal contents over time, the time span was arbitrarily divided into six categories shown in Table 2. Included in this analysis were only those subject classes that had >2% of the total citations.

TABLE 1. The number of citations found for various subject categories in *Northwest Science* between 1927 and 1996.

Subject Category	Subject Matter Included	Number of Articles
agriculture	primarily crop production, irrigation and tillage methods, effects of fertilization	56
amphibians		17
anthropology	primarily Native Americans	8
birds	upland game birds, passerines, raptors, water birds	86
chemistry		42
climate/weather		34
economics		22
education/training		34
fish	primarily salmonids	96
forestry	coniferous species, silvaculture, disease control, re-forestation	242
fire	includes use of fire in site preparation	33
fungi		31
geography	primarily descriptions of places	19
geology	structural and descriptive geology, mineralogy	154
glaciers and glaciation		17
health and human disease		39
hydrology		28
lakes and reservoirs		68
limnology		39
mammals	See Table 3	222
plants	primarily non-coniferous species, includes grasses, shrubs individual species accounts	222
physiology	primarily vertebrate	24
rangelands	includes grazing relations of domestic and native animals	64
reptiles		17
soils	both forest and agricultural	77

Discussion

It is clear from an examination of Table 2 that there have been significant changes in journal content over the years. Articles dealing with educational issues and the training of students were much more common in the early days, probably reflecting the orientation of many of the members towards teaching at the high school and college levels. Today these articles are virtually absent. Likewise, articles dealing with agriculture and chemistry have also greatly declined—the latter probably reflecting the development of more specialized journals for that material.

NWS has long been associated with the disciplines of forestry and geology and articles dealing with those subjects predominated all but the last two time periods. Probably the greatest increase in recent years has been in the number of articles dealing with mammals. Almost a quarter of all articles published in the last 25 years have concerned mammalian species. A compilation of the species is given in Table 3. This change may

TABLE 2. Distribution of records by subject category and time period. Figures are the percent of the total number of records in each time period.

Category	1927-39	1940-50	1951-60	1961-70	1971-80	1981-96
records (#)	241	168	166	183	343	533
agriculture	9	7	7	2	<1	<1
birds	2	1	4	1	5	10
chemistry	9	3	4	4	<1	<1
education	9	5	<1	0	0	<1
fish	4	<1	0	4	8	10
forestry	15	17	20	14	13	13
geology	15	9	9	19	6	6
history	5	2	2	3	2	2
mammals	<1	1	4	4	23	24
plants	7	11	5	13	18	18

TABLE 3. Distribution of mammal studies between 1971-1996 among classes of mammals.

Category	Example Types	Percent of Studies (1971-1996)
small mammals	mice, shrews, voles, pocket gophers, moles, woodrat	40
mid-sized mammals	rabbit, badger, ground squirrel, mountain beaver, porcupine, skunk	16
large grazing-browsing mammals	black and white-tailed deer, elk, moose, mountain caribou, mountain goat, bighorn sheep	28
bears and carnivores	black and grizzly bear, coyote, fox, wolf, bobcat, cougar	13

in part reflect a positive feedback, i.e., one paper on a given subject encourages others to submit additional papers on the same subject. However, a more important factor, in my opinion, is that there is a growing cadre of ecologically trained scientists (and an ecologically oriented public) in the Northwest resulting in more studies of natural components of ecosystems, be they birds, fish, mammals, or flora. This trend can be seen in the pages of NWS along with a diminishment of contributions from the physical and laboratory sciences, as well as engineering, economics, social science, health, and history. Again a negative feedback may be operating here, i.e., a lack of papers in a discipline area discourages readership and submission of papers from individuals in those disciplines.

Given this strong and probably on-going trend, I believe that NWSA should reconsider its mission. The society needs to question the premise, in this era of increasingly fragmented disciplines with a wide variety of scientific journals, of whether it is possible for a society to cover all disciplines. Is NWSA, as currently structured, relevant today? If the journal is an accurate reflection of member's interests (and indeed at least one author of an article must be a member), then I would argue that the society and the journal is not relevant today to chemists, physicists, economists, historians, agricultural scientists, and a host of other disciplines embraced by NWSA. Perhaps changes in the mission of NWSA to more clearly focus only on the biological/ecological sciences are both desirable and necessary to preserve and enhance the society.

Book Reviews

Degrees of Disaster: Prince William Sound: How Nature Reels and Rebounds
Jeff Wheelwright, 1994, Simon & Schuster, New York, New York (348 pp., $24.00 hardbound).

Jeff Wheelwright's book is a nested story of three things—Prince William Sound, the *Exxon Valdez* Oil Spill of 1989 and the subsequent attempts to assess damage, and finally a perspective of this spill as an event in a system that is in continual natural physical and biological flux. Prince William Sound in south central Alaska encompasses vast marine waters and is many things to many people, but rarely the same to all. Its landscapes, defined by glaciers, mountains, rivers and ocean, are home to diversity—of flora and fauna, of peoples, of old and new. This is a snapshot of Prince William Sound.

But to most, the Sound is known for one event, the *Exxon Valdez* Oil Spill. Like the Sound, there is no common perspective on this event. From the start, and to this day, people have many different and often conflicting views. The spill drew worldwide attention—as 11 million gallons of crude oil spilled and spread through its waters; as local communities and federal and state agencies scrambled to minimize damage; and as biologists struggled to assess the short and long-term harm to the Sound's resources. And like the Sound and the spill, Jeff Wheelwright's book is one of diversity and will likely be different things to different readers. His first chapter, "The Earthquake and the Orangutan," has beautifully written and insightful prose that paints a picture of the history of natural physical and biological flux in the system. I was captured by his ability to describe the responses of the Sound to the dramatic disturbances it has faced through time and the difficulties we have in assessing the impacts of a single event in light of this flux. "The ecologist, the oceanographer, the meteorologist, building their theories upon observation, are almost never in control of the variables. They do not even know what all the variables are. Exceptional signals, like the splash of the '64 earthquake or the '82-'83 El Niño, stand out in the Sound and ripple for awhile, but most others are subject to inference. When environmental scientists do design an experiment to isolate a signal, their models... are criticized as too-quiet, too-crude substitutes for the real thing." He artfully tells the story of many of these events and the story of natural variability.

However, his other three chapters are not as effective. The two middle chapters, "Oil and Water" and "Chemophobia " frustrated me. It was particularly in "Oil and Water" that I lost a clear view of who Wheelwright's intended audience was. Was it the scientist, public, policy maker? Unfortunately, while there are parts of this book that will inform each of these audiences, I doubt any will be consistently held by his story. Unlike the diversity and variability that he describes so well as the core of the Sound's ecosystem, it is Wheelwright's diversity in message that will undermine the value of the book for many. "Oil and Water" is a frustrating mixture of the events of the spill and lectures on the nature of oil spilled in water and hydrocarbons. At one point the author provides a paragraph description of chromatography/mass spectrometry, then goes back to the events of the spill. These disruptions detract from the flow of the book. "Chemophobia," seemingly less plagued by this mixing of focus, is a chapter that effectively condenses the confusing and complex story of the assessments of biological damage throughout the "spill ecosystem" from the oil spill clean-up crews breathing fumes to the bald eagles, mammals, fish and bacteria. The author does not support statements with references, but uses phrases such as "Spies told me..." or "Craig Matkin was convinced...". As scientists, readers may be uncomfortable with the lack of referencing and suspect of the statements that follow. However, this is not a scientific treatise, but a nonfiction piece of literature. Keeping that thought in mind is not always easy. The last chapter ends with an emphasis that prevailed throughout the whole spill period, on the sea otter. Perhaps this is appropriate given the "great lengths to rescue and rehabilitate the otters from the oil, and to study the disaster's acute and chronic effects on the animals." The author effectively lays out the pre-spill history and ecology of sea otters and subsequent rehabilitation and damage assessment efforts, both in their biological and human elements.

In the end, is *Degrees of Disaster* worth reading? It won't be an easy read, but I would say try it. Despite its faults, it represents one of the few sources of information about the events of the *Exxon Valdez* Oil Spill outside of the technical literature. Perhaps the best audience for Jeff Wheelwright's book is the upper-level undergraduate and graduate student. Combined with readings from the technical literature, *Degrees* could make the core for a seminar in the trials and tribulations of impact assessment.

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Trees in Canada

John Laird Farrar, 1995, Fitzhenry & Whiteside Limited, Markham, Ontario, Canada and the Canadian Forest Service, Natural Resources Canada, Ottawa. ($40.00 Cdn)

Trees in Canada is a wonderful reference, and this hard covered book is a steal at $40.00 (cdn). The layout, type setting, color photographs, black line drawings and keys make it particularly easy to use. For those of us who relied on its predecessor, *Native Trees of Canada,* the improvements are readily apparent and welcomed.

Specifically, *Trees in Canada* now contains over 300 species and includes for the first time commonly planted or naturalized trees (i.e. Nordmann fir, Siberian larch, Scots pine, and to my surprise, bald-cypress). For added convenience, all trees are stratified into 12 Groups, and these groups are identified on the endleaves inside the front and back covers of the book. Red colored markings are used to show where these Groups appear in the book. This system is efficient and helpful. However, as in previous versions, the trees are also stratified in the table of contents by "The Conifers" and "The Broadleaf Trees", for those who may have found that format helpful. The two page per species layout has also been maintained, at least for all of the major native Canadian tree species, and Rowe's map of the Forest Regions of Canada has also been retained. New additions are: the maps of the Eastern and Western Plant Hardiness Zones in Canada, "Keys to Groups and Selected Genera", "Winter Keys to the Genera", a listing of "Botanical Authors", and a section titled "Meanings of Tree Names". To my knowledge, these additions are firsts for a book of this kind. Also for the first time, there are "Quick Recognition" tips for all the native tree species. I found these last three additions particularly informative and helpful, and they contribute to the value of this book as a teaching resource.

There are a large number of color photographs, in many cases over three per species for the most common of trees. In all cases, the photographs are of "coffee table" quality, and all significantly contribute to helping the user identify the species being described. In addition, there are a large number of black line drawings of features important to accurately distinguish among species within genera. When important, the scale of the drawing is shown. The author even included silhouettes for the various trees described and a key that easily enables the reader to estimate tree heights at a glance.

What I did not like about the book was the fact that species maps do not accurately show the true range of the species. For example, from what is presented in this book, one might conclude the range of *Pinus contorta* Dougl. ex Loud. var. *latifolia* Englem. only extends as far south as Wyoming, which is wrong. However, to the credit of this book, one should know that the tree distributions in the previous versions stopped at the borders between the US and Canada. It would appear that this time the author is trying to be more inclusive. However, I suspect from his perspective one has to decide where to cut off these distributions. Some of the species in this book are found in Mexico and elsewhere.

I am the kind of guy who loves to view, and when possible, identify trees. When visiting a new area of the continent I take the time to identify a few new trees. I find "tree viewing" to be more fun than "bird watching", largely because trees tend to remain in place long enough for me to get the job done. Because of this interest, I have bought more than a few tree identification books. In my opinion, *Trees in Canada* is now one of the better books in my collection, so I recommend it without reservation to all botanists, greenhouse operators, landscape architects and nature enthusiasts. However, readers should know this is a serious tree identification book suitable for any course in dendrology. The descriptions are accurate and clear. The added bonus is that it is easy to use and beautiful to browse through. It will be as welcomed on your coffee table as on your bookshelf.

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Cedar: Tree of Life to the Northwest Coast Indians

Hilary Stewart, 1994, University of Washington Press, Seattle

Elaborately carved cedar totem poles, bentwood boxes, longhouses and canoes are the icons of the people of the Northwest Coast. Perhaps as far back as 6000 years ago, when the cedar tree first arrived in the Northwest, the people living along the coast of southern Alaskan, western British Columbia, and as far south as Washington, have embraced this vital resource in all aspects of their lives. In *Cedar: Tree of Life to the Northwest Coast Indians*, Hilary Stewart successfully tells this story of the cedar tree and its integral part in the lives of the Northwest Coast Indians.

Similar in style to Stewart's *Indian Fishing: Early Methods on the Northwest Coas*t, and *Artifacts of the Northwest Coast Indians*, this book is replete with illustrations and detailed descriptions of cedar artifacts and activities. Stewart skillfully weaves the reader into her descriptions of the traditional uses for cedar, from the heartwood out to the bark and withes, and down to the roots. Beginning with a botanical description of the cedar tree, she discusses the procurement processes, then describes the ethnographic, historic and contemporary uses of the products of this tree, so vital to the coastal peoples that it is known as Long Life Maker.

Well known for her illustrations, Stewart accompanies her detailed drawings with specific descriptions of the processes involved in the production of each kind of artifact, from houses to clothing to ropes. Adding to her own vast expertise in the art and culture of the Northwest Coast, Stewart has conducted extensive archival research, museum visits, oral histories, and interviews with elders, artists, archaeologists, anthropologists, and even a paleobotanist. Deftly, Stewart explains the tensile strength of the cedar withe as an introduction to the knowledgeable ways these branchlets were cut, not twisted, from the tree during the spring, when the withes are most flexible. With warmth and sensitivity, Stewart intermixes scientific descriptions with rich stories and interpretations from the people whose lives, in part, depended on the cedar tree for hundreds of years. No aspect of the cedar tree appears neglected, as Stewart discusses everything from cedar diapers to canoe prows to spiritual guidance on a whale hunt.

At times, Stewart boldly describes technologies and activities that may reach thousands of years into the past. However, she is careful to incorporate archaeological clues to support her interpretations, citing local archaeological sites where worked cedar has been recovered and dated as far back as 5000 to 6000 years.

One of the most difficult aspects for anyone writing on the subject of Northwest Coast peoples is the diversity of artifacts and activities among culture groups. As a result of the available resources and climatic variations, as well stylistic choices, the differences can be vast among the Tlingit, Haida, Tsimshian, Bella Coola, Kwakiutl, Westcoast, Makah, Quileute, and Coast Salish. Stewart tackles this task with success, illustrating and contrasting the distinctive styles of houses, canoes, baskets, and numerous artistic variations. The result is sometimes overwhelming; the lists of different canoe measurements is dizzying, for example. Stewart accomplishes the task, best, however, when she presents other voices; it is the anecdotes, recollections, and personal accounts from individuals of the various culture groups, that contributes the most to the understanding of the complexities of the Northwest Coast cultures.

Perhaps Stewart's greatest strength in *Cedar* are her personal experiences. Adding to the many hours she spent interviewing experts, and researching at museums to complete this book, she has witnessed and participated in many of the activities, including gathering, processing, and the manufacture of the artifacts she describes.

Editorially, the book is nearly perfect. And, like her other illustrated books, she provides a simple, clear reference guide to all her drawings, indicating the sources and cultures. The book, though dense with specifics, is accurately detailed and a pleasure to read. Stewart has once again created a book that is accessible to all, and, like the cedar tree, is vital to those interested in the cultures of the Northwest Coast.

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Biological Degradation and Bioremediation of Toxic Chemicals

G. Rasul Chaudhry (ed.), 1994, Dioscorides Press, Portland, Oregon ($69.95)

Over the past decade, bioremediation, the use of microorganisms to clean toxic chemical-contaminated soils and waters, has become a generally accepted technology, particularly as it relates to cleaning environments contaminated with petroleum hydrocarbons. Today, bioremediation is also being used to clean sites contaminated with numerous other recalcitrant chemicals, ranging from polychlorinated biphenyls (PCBs) to explosives such as trinitrotoluene (TNT). In this book Editor G. Rasul Chaudhry has brought together many of the leading researchers in the bioremediation field, and they have authored a selection of excellent chapters covering the breadth of this complex topic.

Chapter 1, by Houghton and Shanley, reviews the potential of the Gram negative pseudomonads, one the catabolically most versatile bacterial groups, for use in bioremediation of aromatic chemicals. Importantly, the authors emphasize not only the catabolic potential of these bacteria, but also their genetic plasticity and abilities to adapt genetically to the utilization of recalcitrant organic compounds as sources of carbon and energy. The authors emphasize the fact that pseudomonads are adaptive largely because of the ways in which they globally regulate their pathways in the presence of mixed substrates, particularly when they are under selective pressure. This chapter sets a good tone for the rest of the book.

Chapter 2, by Furukawa, examines soil bacterial degradation of PCBs. Pointing out that PCB-degrading bacteria are ubiquitous in the environment, the author discusses synthetic PCB degradation as a phenomenon originating from the natural ability of soil bacteria to degrade natural biphenyl-like structures. Like was done in Chapter 1, Dr. Furukawa discusses how genetic plasticity, adaptation, and gene transfer are involved in the process by which bacteria acquire the abilities to utilized PCBs.

Chapter 3, by Sylvestre and Sondossi, carries this concept to the next level, or the use of selective pressure to develop enhanced PCB-degrading bacterial strains for use in bioremediation of soils and sediments. Selection strategies based upon our accumulated knowledge of bacterial catabolic pathways for chloroaromatic compound degradation are discussed, the goal being to introduce gradual genetic modification in the relevant bacterial pathways in order to systematically improve the bioremediation efficiency of specific bacterial strains. Thus, Chapter 3 is a logical follow-up to the two previous chapters.

Chapter 4, by Hale, Reineke and Wiegel, reviews biodegradation of another class of chloroaromatic compound, the chlorophenols. Chlorophenols such as pentachlorophenol (PCP) are wide spread environmental contaminants in soils, sediments, and aquifers. Aerobic and anaerobic chlorophenol degradation pathways are thoroughly, yet concisely reviewed. In this chapter the authors emphasize intermediary metabolism more than they do genetics.

Chapter 5, by Pothuluri and Cerniglia, reviews microbial metabolism of polyaromatic hydrocarbons (PAHs). Like chapter 4, the authors emphasize intermediary metabolism, pathway sequences, but also enzymology. This excellent review should prove to be a useful reference for students and established researchers alike. In particular, I liked the sections on most recalcitrant of the PAHs, such as benzo(a)pyrene and benz(a)anthracene.

Chapter 6, by Gilluray and Shiaris, complements chapter 5, by looking at PAH biodegradation in one particular environment, coastal sediments. The approach of the authors was to examine the phenomenon from an environmental condition and microbial ecology perspective. This is a solid contribution to the book, though much more focused than the first 5 chapters.

Chapter 7, by Hale, Jones, and Rogers, examines the biodegradation of chlorinated homo- and heterocyclic compounds in anaerobic environments. This is a hot area of research currently, and the review is timely. The authors discuss the process of reductive dechlorination of these compounds in anaerobic environments, and the importance of this to complete biodegradation of these compounds. They also discuss the aromatic ring substitution preference for reductive dechlorination, the resulting differences in biodegradability of different compounds, and the strategies that might be applied to bioremediating anaerobic environments contaminated with various of these recalcitrant chemicals.

Chapter 8, by Hooper, shifts to another chemical class, the sulfonated aromatics, such as sulfonated azo dyes, sulfonated naphthalenes, linear alkylbenzene sulfonates, and benzene sulfonates. These chemicals are surprisingly important environmental contaminants worldwide. The author has written an excellent contribution that summarizes the widely dispersed literature on this topic. Importantly, he discusses degradation with an emphasis on pathways, and on pure cultures versus consortia in both aerobic and anaerobic environments. One area he did not cover was recent work on peroxidase-mediated degradation of sulfonated azo dyes.

Chapter 9, by Venables and Knapp, is very focused, on the biodegradation of morpholine, a heterocyclic compounds used widely as an industrial chemical. The authors discuss the finding that morpholine degradation appears to be a common property of the mycobacteria, a group that is difficult to work with when developing bioremediation and waste effluent treatment strategies and processes. Since morpholine degradation appears to be plasmid encoded, the authors proposed that the develop of more competitive recombinant strains other than mycobacteria might be pursued.

Like chapter 9, chapters 10 (Mateen et. al.)and 11 (Behki) are focused on discussions of biodegradation and bioremediation of specific chemicals or chemicals types. These include biodegradation of the carbamate and organophosphate pesticides (Chapter 10), and degradation of the thiocarbamate herbicides by rhodococci (Chapter 11). There is a wealth of information in these chapters.

Chapter 12, by Montgomery et al., covers the important and timely topic of anaerobic biodegradation of chlorinated organic compounds. Reductive dechlorination is discussed as the Major mechanism involved in biodegradation of these compounds anaerobically. This chapter complements and expands on the information found in chapter 7. The authors also discuss the strategy of anaerobic, followed by aerobic degradation as a bioremediation approach for degradation of some of the most recalcitrant and highly chlorinated compounds. Of particular value to students is the discussion of reductive dechlorination mechanisms, enzymology, and energetics.

Chapter 13, by Hanson and Brusseau, complements chapter 12 by focusing on biodegradation of low molecular weight halogenated organic compounds, some of which are degraded only via cometabolism. While biodegradation of each of the classes of these chemicals is reviewed, there is an emphasis on the compounds of most importance as environmental contaminants. Chief among these is, of course, trichloroethelene (TCE). The involvement of methanogens in the cometabolic degradation of TCE is thoroughly reviewed. There is also an emphasis on the potential for using molecular ecology methods for examining the factors controlling populations of methanogens in the environment, and therefore, for optimizing cometabolic bioremediation of TCE.

Chapter 14, by Gibson and Harwood, examines anaerobic biodegradation of aromatic carboxylates, including both natural and synthetic compounds. The importance of this chapter is in its emphasis on anaerobic biodegradation pathways and on our limited knowledge of the enzymology involved in degrading aromatic compounds such as lignin, particularly in the absence of oxygen. Both chemoheterotrophic and phototrophic metabolism are reviewed. Finally, strategies for bioremediation of aromatic carboxylates in anaerobically are discussed. This chapter is an excellent on in terms of not only the review of the topic, but also in the broader perspective it gives the reader.

Chapter 15, by Henry and Grbic-Galic, complements chapter 13, since it also examines the cometabolic biodegradation of TCE. There is an emphasis in this chapter on field bioremediation research results. Thus, it is somewhat more applications oriented than was chapter 13. However, the review of TCE metabolism and enzymology is excellent.

Chapter 16, by Orth, Pease, and Tien, examines the possibilities of using the well studied extracellular lignin and manganese peroxidases of the white-rot fungus *P. chrysosporium*, for bioremediation of a wide variety of xenobiotic compounds. The material covered is primarily basic information on the properties of the enzyme and the free-radical generating mechanisms by which it oxidizes lignin and xenobiotic compounds. There is some discussion of how the enzyme is produced and what needs to be done to enhance production if the enzyme is to be used successfully for

bioremediation. From a basic information standpoint, this is an excellent chapter. From the bioremediation standpoint, the authors' review shows that actual use of the enzyme for xenobiotic destruction in the field is far from a reality.

Chapter 17, by Chahal, turns to the subject of lignocellulosic wastes as environmental contaminants, and to biologically treating them to reduce their toxicity. The chapter actually looks at two alternatives for treatment of crop and timber, wood processing , and pulp manufacturing wastes. The first is biodegradation, while the second is bioconversion to alternate, useful products. This review provides basic information on the structures of lignocellulose components and the lignocellulose complex itself, and on the enzymology of lignocellulose degradation. This is useful information for students starting out in this area of research. There is also a good review of what types of bioconversions have been developed using lignocelluloses as starting substrates for microbial conversion. As is clear from reading this chapter, there is much potential for this technology, though it has not been realized very well to date.

Following in the footsteps of chapter 16, is Chapter 17, by Fernando and Aust, on the biodegradation of xenobiotics by white-rot fungi. This fungal group includes *Phanerochaete chrysosporium*, but many additional potential fungal species as well. The conclusions drawn by the authors are that the white-rot fungi are versatile xenobiotic degraders, and it should be possible to develop effective bioremediation processes that utilize them, usually starting from an inoculum raised on some organic substrate like wood chips. Though the potential has not been fully realized, successful bioremediations using white-rot fungi have been demonstrated in the laboratory and field from a few fungal species.

Chapter 19, by Ohtake and Silver, turns to the subject of microbiological heavy metal detoxification, as applied to chromate. The concept here is to use microorganisms to detoxify (e.g., reduce) and immobilize chromate within the environment. This chapter is basically a good review of what is known about biological chromate reduction. Some application possibilities are discussed towards the end of the chapter.

Walter Reineke, in Chapter 20, examines strategies for strain development as a way of improving specific microorganisms in their abilities to biodegrade/bioremediate chloroaromatic compound degradation. The chapter recovers some material present in previous chapters, though the review is well and concisely written. The latter part of the chapter deals with microbial isolations strategies (e.g., enrichment) and strain development (e.g., *in vitro* construction using recombinant DNA procedures, and *in vivo* construction using selective pressure). There is an extensive table summarizing relevant genes that have thus far been cloned, and how they might be used to develop superior bioremediation strains. Also present is a similar table summarizing. While the chapter may not contain a lot of "new" information for experienced workers, it will be valuable as a information source for students.

In Chapter 21, Levinson et al. discuss the possibilities for hazardous waste cleanup and treatment using encapsulated or entrapped bacterial cells. The advantages and disadvantages are reviewed, and a number of novel encapsulation/entrapment techniques are described. The authors point out that this technology often markedly improves bioremediation results in the field (particularly *in situ*), and encapsulation is now almost a commercial reality in some applications. Improvements in bioremediation results appear to be resulting largely from enhancement of microbial survival, particularly in soil. Much of the research data provided concerns the use of encapsulated or entrapped *Flavobacterium* cells to degrade PCP.

Chapter 22, by Murty et al., reviews current research in the area of coal bioprocessing. It is not out of place in the book, since coal or coal-derived compounds are significant environmental contaminants and hazards. Biodesulfurization of coals is reviewed, as is biosolubilization, biohydrogenation, and bioleaching of heavy metals from coal. There is also an overview of the chemical and molecular structure of the heterogeneous material we know as coal. There is a short section on bioliquefaction of coal, though the differences between liquefaction and solubilization are not made clear. While not all of the literature was covered by these authors, this review is a good starting point for those doing research on this topic.

Chapter 23, by Larsson et al., overlaps chapter 21, but focuses on the use of microbial processes to desulfurize coal, with an emphasis on removing pyritic (inorganic) sulfur. As is clear

from this review, economic pyritic sulfur removal processes are nearing the point of being ready for commercialization. This is one bright spot in a research area where very few are doing research today because of a general lack of interest by funding agencies like the U.S. Department of Energy for "biological" research on fossil fuels.

This is a valuable and timely book that covers this immense field of research fairly well. The chapters are well written and will be useful sources of reference material for researchers. In addition, the book should prove useful in helping researchers and particularly students gain a better overall perspective on the potential uses of microorganisms for bioremediation of xenobiotic-contaminated soils and waters.

It is a book that should not only be in the library, but also in the laboratory close by and available as a reference and idea source.

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Ecological Risk Assessment: Uses, Abuses, and Alternatives

Rosemary Mazaika, Robert T. Lackey, and Stephen L. Friant (eds.), 1995, Amherst Scientific Publishers ($30.00)

Human activities that alter the environment are increasing in frequency, scope, and scale. Print and broadcast media bombard citizens with gloom and doom scenarios about the consequences of environmental change for health and quality of life. Recognizing that conservation efforts which attempt to limit environmental change may have adverse effects on certain sectors of the economy (e.g., timber workers), people are requesting thoughtful assessments of the likely effects of various activities which impinge on the environment. In large, they simultaneously want a healthy environment and healthy economy, and are seeking information useful in striking this balance. These conditions have led to recent and widespread interest in the field of ecological risk assessment (ERA).

Ecological Risk Assessment: Uses, Abuses, and Alternatives comprises a set of thoughtful papers articulating a variety of philosophies concerning environmental decision-making. The book is a hard-bound copy of a special issue of the journal *Human and Ecological Risk Assessment* (published by Amherst Scientific Publishers in October, 1995) with fourteen short papers from a symposium on ecological risk assessment held at Oregon State University in November, 1994. Presumptive themes of the papers include: the ecological risk assessment paradigm (3 papers), risk assessment in practice (2 papers), risk assessment and politics (3 papers), alternatives to ecological risk assessment (3 papers), and the future of ecological risk assessment (3 papers).

Unlike the spate of recently published "how-to" books on performing ecological risk assessments (Bartell et. al., 1992; Calabrese and Baldwin, 1993; Maughn, 1993; Suter, 1993), very few papers provide technical information useful to ERA practitioners. Instead, papers deal with the larger issues regarding the nature of environmental decision-making in Western society, and the usefulness of ERAs as tools to enhance the decision-making process. In fact, upon reading the book one is left with the impression that there is so little consensus on the objectives and value of ERAs, that discussions of methodological issues is tantamount to "putting the cart before the horse" (although I am convinced that scholarship regarding the technical aspects of ERAs are of substantial value). Certainly, open discussion of the underlying philosophical roots, political and economic context, and the role and value of ERAs in society is particularly useful near the genesis of the discipline. This book may serve as a useful primer for such a debate.

Below I give a brief descriptions of each paper, for the book itself has no preface to inform readers of content. Following these descriptions, I briefly review some common themes and recurrent misunderstandings that give the appearance of greater divisiveness on the issue of ERAs than may actually exist. I think clarification of a few common misconceptions may allow more profitable discussion of the important outstanding issues regarding ERAs. Naturally, all reviewers carry personal expertise, biases, and values that shape their attitude of quality. Therefore, I feel it important to state from the start that I am an ecologist and carry the associated biases of a practicing scientist.

The book opens with an overview by Robert Lackey in which he aptly identifies two key points that stand at the center of the apparent controversy over the use of ERAs: 1) an individual's world view, and 2) the perception of who pays the cost and receives the benefits of environmental policy decisions. In the next paper, James Regens discusses several methodological issues such as whether the risk assessment process is adequate to make timely policy decisions with minimal uncertainty, the importance of making necessary assumptions and judgments as transparent as possible, selection of biologically relevant endpoints that can be accurately measured and are sensitive to the perturbation(s) being assessed, and choosing the proper scale and level of biological organization (population, community, ecosystem) to be assessed. Dorothy Patton follows with a well-written summary of the U.S. Environmental Protection Agency's (EPA) recent efforts to construct a framework for ERAs. She discusses the objectives of the EPA work, how and why it was performed, and outlines the important elements of ERAs. It is clear that the EPA framework reflects commonsense problem-solving and decision-making, and as Patton reflects, much

of the apparent controversy over the process may be due to misunderstanding and miscommunication. Ecological alternatives assessment is presented as an alternative to ERAs by Mary O'Brien. She argues that the moral premise upon which ERAs are based is wrong (it is ethically wrong to harm the Earth), and that the assessment process is unscientific because it is based on the single-chemical risk assessment paradigm. She suggests a proactive approach where technical and social alternatives are discussed prior to risk assessments, and policies that lead to minimal long-term environmental damage are pursued. In a paper by Anne Fairbrother, Lawrence Kapustka, Bill Williams, and Jessica Glicken, the risk communication and decision-making process is discussed within the context of Western socio-economic systems. The paper cogently outlines how and why *a posteriori* environmental management efforts (e.g., ERAs) are limited but important elements of capitalistic democracies. They also discuss the role and nature of public involvement in the risk-management process. For several reasons similar to those discussed by O'Brien, Joel Pagel also introduces ecological alternatives assessment as a better method of environmental decision-making than ERAs. He argues that natural systems are so complex that it is misguided to think we can meaningfully assess the likely effects of anthropogenic perturbations.

Led by Richard Clinton's short piece outlining the struggles and benefits associated with decision-making in democratic political systems, a couple of papers discuss the role and nature of ERAs and other decision-making tools in democracies. E.J. Woodhouse argues that politics is superior to science as a method for making complex decisions, and suggests the EPA may be advancing ERAs as a political tactic because the process appears scientific and cost-effective to administrators. Perhaps the most interesting aspect of the paper is a discussion of "trial and error" policy-making for handling environmental problems that are plagued with considerable uncertainty. Ted Schrecker emphasizes that environmental decision-making involves negotiation among citizens with varying values about what constitutes risk. Because ERAs involve considerable uncertainty and require numerous assumptions, scientists may impart their biases and values when assessing and communicating risk. Therefore, care must be taken to insure assumptions are critically reviewed and that ERAs are constructed in a manner relevant to policy debates.

The final set of papers deals loosely with the future of ERAs. Ellen Hayakawa advocates multi-stakeholder involvement in environmental decision-making because it empowers individuals and promotes collective environmental citizenship and stewardship more effectively than top-down decision-making. Ecological benefits assessment, a process discussed earlier in the book by O'Brien and Pagel, is best explained by Peter Principe. Principe discusses the conceptual differences between a benefits assessment and a risk assessment, and outlines the basic elements of the benefits assessment process. He provides several clear example of how the process may contribute to decision-making. James Karr argues that current conceptions of ERA are unlikely to effectively limit current and widespread ecological degradation. He suggests the goals of ERAs must be defined more broadly to protect Earth's life-support systems, and thus human well-being which is dependent on these systems. These goals may be better accomplished through place-based environmental management "designed to integrate ecological systems and the human economies dependent on those systems" in a geographic region. According to Odelia Funke, ERAs have several scientific, socio-cultural, and philosophical limits. The scientific limits stem from the fact that ecological systems are poorly understood and difficult to predict. Funke also writes an interesting description of the roots of Western value systems and how these values shape our approach to environmental decision-making. Finally, Paul Merrell suggests that risk assessments are frequently concocted to produce whatever outcome its promoters wish.

Perhaps the greatest shortcoming of the book is the lack of any substantive organization. An opportunity to highlight important issues worthy of continued thought and debate was compromised by the decision not to include a preface or introductory and summary chapters that emphasize similar themes and divergent opinions on a particular issue. For example, at least four papers (O'Brien, Pagel, Principe, and Karr) discussed a purported alternative to ERAs that appeared to share the view that ecological alternatives or benefits should be assessed as opposed to risks. Although there appear to be several differences among

these authors on their view of this alternative process, many elements discussed in the various papers were similar. Because the authors used different terms for the process, an introduction or other organizational tool highlighting the common message of these papers would have significantly reduced reader confusion.

Several common messages are repeated throughout the book. For example, virtually all authors argued that environmental decision-making must incorporate the values of stakeholders. Most papers suggested the goals of assessments should be constructed based on an open political debate because "risks" and "benefits" are ultimately defined by the citizenry in democratic societies. Similarly, use of assessment results in policy determinations must also reflect the values of society. However, the authors presented less consensus on public involvement in the technical aspects of risk assessment. Fairbrother et. al. advocate that technical aspects are best left to objective scientists, while Schrecker argues that scientists carry common personal biases which can affect the outcome of assessments, and therefore, assumptions and scientific judgments should be openly debated. Also, most authors recognized that predicting the response of ecological systems to anthropogenic perturbations is extremely difficult and uncertain. As the scale of the assessment increases (e.g., population vs. ecosystem), uncertainty increases, suggesting that ERAs are most effective for relatively small-scale problems (Regens, Principe).

Perhaps unsurprising, terming the problem-solving process as ecological *risk* assessment appeared to have resulted in considerable miscommunication. As a result, many of the apparent controversies are due to differing opinions of the objectives of an ERA. The concept of "risk" is value-laden, risk depends on ones view of what constitutes an adverse effect. However, the technical process of evaluating environmental effects is much less burdened by personal value judgments. Quite simply, the technical aspects of the assessment involve scientists and other practitioners attempting to describe how biological components of systems respond to a disturbance regime (e.g., pollutants, pesticides, timber harvest). Although value judgments such as whether to use a central tendency measure (e.g., mean, median) or lower 95% confidence interval to parameterize a particular input are necessary, these debates are seemingly much less contentious than the broader problems of how to use analytical results in policy decisions. However, because the process has been termed a risk assessment as opposed to an effects assessment, many authors assumed that the goal of the process is to optimize the "taking" of a resource. While this may be an objective of some assessments because framers of the assessment seek such output, it is not a necessary objective for the process. Stakeholders may define the objectives in many different ways, and similarly, stakeholders may use the results in a variety of manners. However, the fundamental nature of the assessment process as described by Patton and others will remain relatively unchanged. This is so because the process itself is based on time-tested, conventional scientific investigation. Unfortunately, miscommunication about the fundamentals of effects assessment led to cynicism (Merrell) and unnecessary confusion.

With the possible exception of Principe, the authors discussing ecological benefits assessment explicitly presented the process as an alternative to ERAs (O'Brien, Pagel, Karr). I think this contrast may have introduced a false dichotomy. I see the two processes as related, but fundamentally different decision-making tools. As inferred by Patton and Regens, an ERA is a commonsense, pragmatic method of inquiry and problem-solving. ERAs seem best suited as an *a posteriori* environmental management tools, especially when environmental problems are few or narrowly defined (see Fairbrother et. al.). In other words, they are best suited for the important role of handling existing problems (or assessing the effects of a restricted set of future environmental changes) which will always be prevalent in society. Ecological benefits assessment is better described as an *a priori* management tool (Fairbrother et. al.). Benefits assessment is a proactive process requiring citizens to reach consensus on a common vision for ecosystems or landscapes. Once this vision is articulated, alternative policy options for achieving the goal are assessed. In all likelihood, ecological benefits assessment will incorporate numerous ERAs, although the process may be renamed "ecological effects assessment" to eliminate the value-laden "risk" term (Principe). In short, the two processes are not really substitutable, they serve separate and important functions. In no way does this clarification diminish the larger message of the O'Brien, Pagel, Principe, and Karr

papers. Instead, their papers better argue for more emphasis on *a priori* decision-making as a means of constructing environmental policy. Such forward-thinking environmental management will likely reduce the frequency of ERAs in the future.

The organizers of the conference performed a laudable job of bringing experts from a variety of disciplines to make contributions. However, I feel that the discipline of ecological risk assessment could benefit from the insights of business scholars familiar with the theory and practice of decision-making in an uncertain world. Although Woodhouse touched on these methods, more comprehensive treatment of decision-making under uncertainty would be profitable.

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In summary, the book can provide a useful tool for stimulating discussion about the role and nature of environmental decision-making in democratic societies. It offers succinct discussions of the primary problems that effective environmental policy must resolve (e.g., diverse stakeholder values, uncertainty). However, it provides little information useful for the technical aspects of assessing ecological risks.

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Wildlife and Recreationists: Coexistence Through Management and Research

Richard L. Knight and Kevin J. Gutzwiller (eds.), 1995, Island Press, Washington, D.C. ($49.95 hardcover, $27.50 paperback)

Recently, I saw an osprey dive into the icy waters of a Cascade mountain lake and fly away with a trout wiggling in its talons. The few seconds that passed as the osprey caught and secured its lunch were the highlight of my hike and will stand in my memory long after the rest of the day fades. Like many recreationists, my experience had been enhanced by an encounter with wildlife. However, after reading *Wildlife and Recreationists*, I wondered what role, if any, that my presence had played in the vignette. Was the osprey's fishing limited because it was avoiding the waters near the shore where I stood? Or was the fishing enhanced because the trout had seen my movement along the shore and moved out into open water? Every day, natural-resource managers are faced with these types of questions and expected to make policy decisions based on their answers. In turn, they often ask researchers to design studies aimed at answering the questions and guiding policy. For both managers and researchers, *Wildlife and Recreationists* is a useful resource.

The title and subtitle of the book describe a lofty goal, the coexistence of wildlife and recreationists through management and research. In addition, the preface states that the book is primarily intended to be of practical use to natural-resource managers who share that goal. However, the primary conclusion fostered by reading the book is that the current state of knowledge is not sufficient to support generalizable recommendations for specific management action. Chapters 7 through 19 do include sections recommending management options. However, there is generally much less specificity and confidence displayed in those sections than in the sections describing knowledge gaps that end those same chapters. This is not to say that the book is of little use—although it is unlikely to provide any managers with definitive answers justifying specific management actions, it could help them better understand the issues that surround interactions between wildlife and recreationists, and could also provide guidance for gathering information that leads to effective management.

The book consists of 21 chapters organized into four sections. *Part I* presents general issues involved in wildlife/recreationist interactions. *Part II* focuses on more specific issues, including aspects of the interaction such as noise, and effects of interactions on animal populations and communities. *Part III* consists of seven case studies that illustrate different types of interactions and some approaches to their management. Finally, *Part IV* presents a brief restatement of options for managing wildlife/recreationist interactions and then concludes on a jarring note with a chapter that rejects the very premise of recreation management.

The organization of the book reflects the limitations of current knowledge concerning wildlife/recreationist interactions and the ways to manage them effectively. Based on the book's title and preface, one might expect a sort of cookbook that provides recipes for managing different types of wildlife and recreational experiences. Instead, the book is made up of nearly independent chapters that discuss the issues in a relatively abstract way. Imagine a real cookbook with the organization scheme described above: it would have no specific recipes but would first focus on general and specific cooking principles, then would describe the processes by which several people developed new dishes, and would end with the conclusion that reliable recipes were beyond the current state of knowledge and that dishes could only be developed on a kitchen-by-kitchen basis. Although it is possible that such a book could have (many years ago) represented the state of the art in cooking knowledge, to the hungry person in the kitchen it would be a resource that was less than ideal but also better than nothing.

The first few chapters illustrate how *Wildlife and Recreationists* is more a description of the current state of a developing field than a cookbook based on established principles. The first chapter defines several types of wildlife/recreationist interactions and discusses the projected demand for recreation that involves such interactions. Then, with no framing text or transition, the second and third chapters discuss concepts and strategic frameworks useful for managing recreationists. All three chapters serve to introduce issues and terms that are critical to understanding and managing interactions and thus provide valuable information to managers and researchers (as do the remaining chapters in *Part*

I). However, there is no attempt to guide the reader from one chapter to the next by explaining how they relate to each other. Perhaps a small introduction to each chapter could have helped tie the book together for the reader. Also, because they were included in *Part I* rather than *Part II*, Chapters 2 and 3 do not include the sections providing specific recommendations of management options. Such recommendations might prove useful to managers interested in modifying visitor behavior.

As in *Part I*, the chapters in *Part II* are largely independent treatments of their topic areas. In fact, there is some overlap in their conclusions and recommendations. In *Part II*, Bowles's Chapter 8 concerning wildlife responses to noise stands out as a particularly thorough presentation of a difficult area of research. It presents a clear discussion of the unique problems faced by researchers investigating noise, a thorough review of the existing research, and a number of general recommendations for management actions. In contrast, Anderson's Chapter 9 seems a notably more cursory treatment of the research concerning recreational effects on wildlife populations. Several unreferenced statements stand out, such as, "Other studies have also shown that as long as hunting is controlled, it substitutes for mortality factors and therefore does not have an adverse impact on a population." (p. 158), and, "There are instances where hunting has caused birds to fly up and hit transmission lines, buildings, or windows as they try to escape the noise." (p. 159) In addition, the statement that one can determine when people are having an impact on a wildlife population by examining mortality rates using life tables is erroneous (p. 165).

Many managers will find the case studies in *Part III* to be the most accessible and useful portion of the book. In particular, Anthony, Steidl, and McGarigal's Chapter 13 describing management of interactions between bald eagles and recreationists on a Pacific Northwest river and Larson's Chapter 15 describing site design and interaction management at a heron rookery in Colorado stand out as useful models for managers. The case studies are also useful in illustrating a range of interactions between recreationists and a variety of animals. Situations are described in which the animals are hunted (Chapters 14 and 19), in which viewing animals is the primary purpose for most recreation at the site (Chapters 15 and 16), and in which the animals may be secondary attractions or may be irrelevant to the recreation motive (Chapters 13, 17, and 18). The chapters also describe situations that vary from tight regulation (Chapter 14) to no regulation (Chapter 19). Finally, the case studies illustrate how managers have translated research results to justify a variety of management actions.

In the penultimate chapter of the book, Knight and Temple briefly describe the actions available for managing wildlife/recreationist interactions. They also state that all management decisions must be made on a site-by-site basis. Such a conclusion, although realistic, is likely to be discouraging to many managers hoping to avoid paying for site-specific research. Their final statement correctly points out that good management decisions will be made by managers armed with good information.

The book ends on a glaringly discordant note with the chapter by Oelschlaeger. After twenty chapters that discuss pragmatic issues of managing for the coexistence of wildlife and recreationists, the final chapter of the book makes a case that it is folly to even consider such areas to be manageable. The author advocates a view of, "therapeutic nihilism— nature knows best and it is a vanity to think humans are in control" (p. 345). Although most readers will no doubt be sympathetic to the view that humans are indeed an integral part of nature, the managers and researchers charged with making concrete decisions about wildlife policies will almost certainly be left cold by the implicit assertion that the one, and only, worthy path to saving the environment is to foster a worldwide philosophical conversion to a "land ethic." Specific recommendations about how such a conversion would blunt the impact of billions of humans on the natural world, or descriptions of policies that should be put in place while we wait for the Truth of the "land ethic" to sweep across the globe, are conspicuously lacking. The final chapter certainly provides a philosophical counterpoint to the rest of the book, but given the goals and intended audience of the book, its inclusion is questionable.

Wildlife and Recreationists is a useful resource for both managers and researchers, but managers are likely to find it difficult to translate the book's conclusions directly to action. The book adequately makes the case for the complexity of the problem

and the need for further research, but it misses an opportunity to explicitly suggest how managers (and applied researchers) faced with small budgets and short schedules can use small research projects to support both management policy and theoretical development. Still, the large research needs described in the book are very real, and the chapter references serve as useful guides to existing research. Both managers faced with issues concerning wildlife and recreationists and the researchers they call upon for assistance would benefit from reading the book. All readers should take care however, not to start with the last chapter and assume that it summarizes, or is even remotely consistent with the rest of the book's contents. Anyone who did so and was intrigued enough to continue would be disappointed by the pragmatic nature of the other chapters, and those who stopped reading at that point would miss a book that makes a genuine contribution to the attainment of the condition described in its subtitle.

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Text: Literature citations within the manuscript text should contain the author's name and year of publication, using formats A and B.

- Format A:
  ...studied by Jones (1978)...
  ...studied by Smith and Brown (1979)...
  ...studied by Smith et al. (1980)... (if more than two authors in a citation)
- Format B:
  ...was previously investigated (Smith 1965, Jones 1971, Harris 1982)...

...results of other investigations (Smith 1966, 1970; Jones 1973; Brown 1974)...

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Present all data in international (SI) unites. English equivalents may be added parenthetically. Use the 24-hour clock (0600 and 2230) and continental dating (17 November 1986).

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Citations should be double-spaced and listed in alphabetical order at the end of the article. Listed below are some typical citations.

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Broadbooks, H. E. 1970a. Home range and territorial behavior of the yellow pine chipmunk *Eutamius amoenus.* J. Mammal. 51:310-326.

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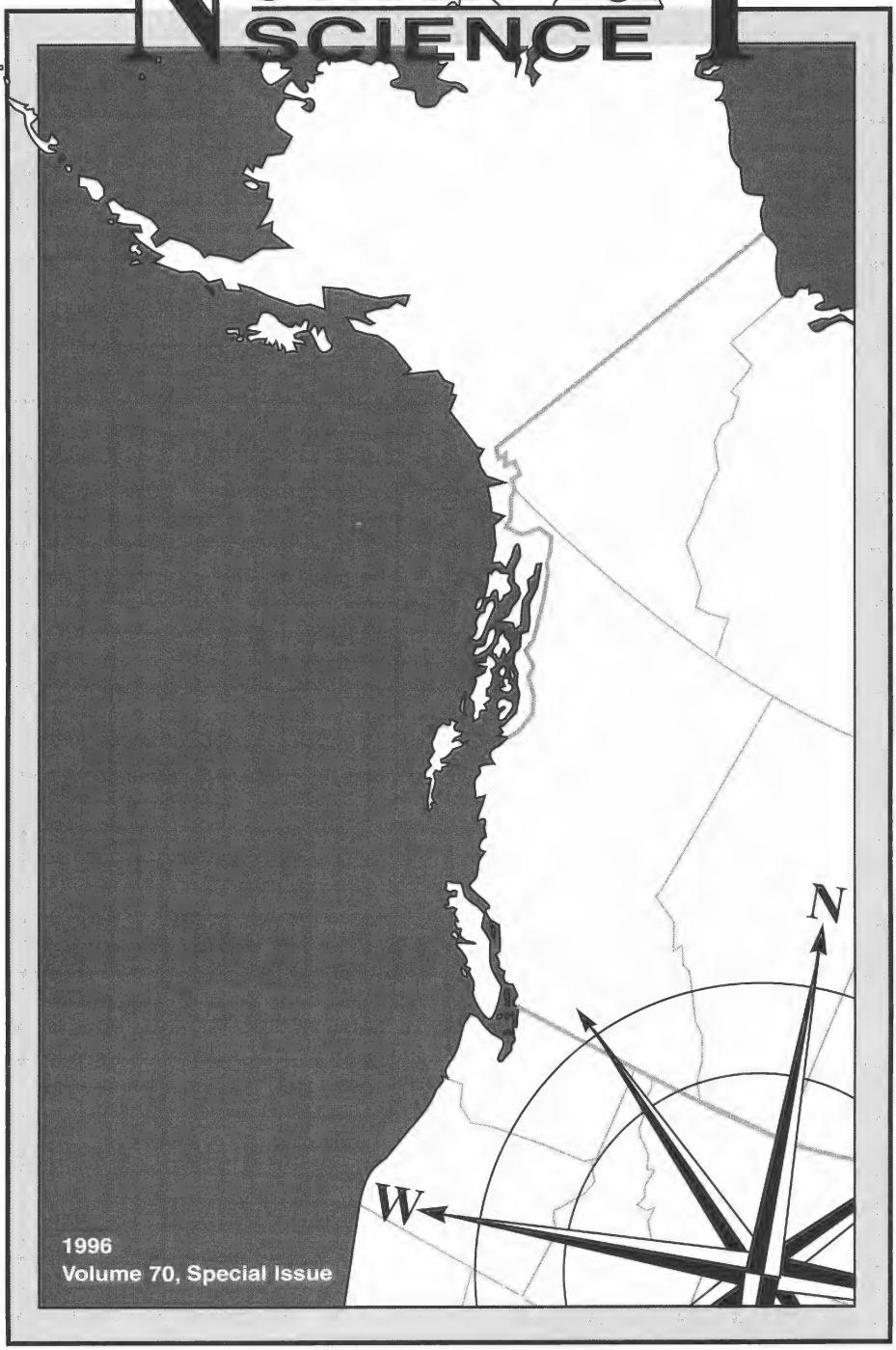

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Editor's Note

The vast majority of our scientific knowledge about forest ecosystems focuses on those components of forests that are easily studied from a technical perspective. We have a wealth of data about above-ground—albeit near-ground—features of forests. We have considerably less information about processes and functions in the forest canopy. The impressive height of forest canopies in many of the lower elevation forest types of the Pacific Northwest poses a special challenge in terms of access and understanding. There has been an upsurge of interest in forest canopies over the past decade or so. Although many of the scientific advances have been in biologically diverse tropical rainforests, there has been interest in North American forests as well. The interaction of forest structure, canopy processes, and biota in forests of the Pacific Northwest is the focus of this special issue of *Northwest Science*. The papers in this issue will serve to inform readers of the status of our knowledge about Northwest forest canopies, and provide a look into the future of research where the forest touches the sky.

Comments regarding this special issue and requests for additional copies should be directed to the Guest Editors. Correspondence about specific articles and reprint requests should be sent to the authors of those articles.

— The Editor

Northwest Science Special Issue 1996

Northwest Forest Canopies

Preface

Standing on a platform in a Douglas-fir tree 55 meters above the forest floor, with 35 meters of canopy still above my head, the difficulty in studying the forest canopy of the Pacific Northwest comes home. I desire wings, like the raven, so I can cruise through the complex and varied openings of the canopy in search of biological wonders. Here in the H.J. Andrews Experimental Forest where forest canopy science was born in the Pacific Northwest twenty or so years ago, we still have only the most rudimentary understanding of the ecology and biology of this sphere of the forest.

Where exactly are we these days, in terms of quantifying and describing the structure of the canopy, of understanding what microfungi, invertebrates, lichens, vertebrates, and other organisms are doing here, of knowing the relationships between structure, function and productivity? How does the forest canopy interface with the atmosphere, affect forest hydrology, influence productivity of streams, and generally influence the environment? Scientific investigators have climbed, put up platforms, towers, walkways, used ladders and scaffolds, and even cranes to study the canopy. In this Special Issue of *Northwest Science* we attempt to draw a picture, albeit incomplete, of some of our current understanding of the biology and ecology of the forest canopy, with special attention to our region.

This Special Issue of *Northwest Science* comes from a symposium held in March of 1994 at the 67th Annual Meeting of the Northwest Scientific Association in Ellensburg, Washington and sponsored by the Ecosystem Research Group at the College of Forest Resources, University of Washington, USFS PNW Research Station, Northwest Scientific Association, and The International Canopy Network. This issue was guest edited by Cathy Rose, Steve Sillett, Andy Carey, and myself. The purpose of the symposium, and this Special Issue, is to raise awareness of forest canopy science and the vital role this interdisciplinary approach will play in our full understanding of forest ecology and management.

The nature of such an interdisciplinary science as this, made it difficult to include many of the subject areas within canopy science for this Special Issue. What we have emphasized here is the biotic elements of forest canopies, as well as aspects of tree physiology and atmospheric interaction, structure, general ecosystem functions, and silviculture. One gaping hole in our biotic coverage is use of the canopy by non-passerine birds, including marbled murrelets, spotted owls, grouse, and hawks. Unfortunately, our planned paper on this subject did not materialize.

Forest canopy science is a rapidly emerging subdiscipline of forest biology and ecology. A new scientific text by Lowman and Nadkarni (1995) and popular books and articles such as Moffett (1994), Wilson (1991), Mitchell (1986), Perry (1986), and Denison (1973), as well as symposia and conferences such as the First International Forest Canopy Symposium held at the Marie Selby Botanical Gardens in Sarasota, Florida in November 1994, are propelling the subject into the forefront of science. Within the Pacific Northwest, a 75 meter tall construction crane has been installed at the Wind River Experimental Forest, Gifford Pinchot National Forest, Washington. The investment in such a research facility is significant, and has begged the question, "Why study the forest canopy?". I (we) hope this Special Issue answers that question.

The definition of forest canopy is often debated, and no official definition has been established. It is often considered the upper forest roof or the upper parts of tree crowns, as in an overhead covering. Geoffrey Parker (1995) defines the canopy as, "the combination of all leaves, twigs, and small branches in a stand of vegetation; it is the aggregate of all crowns."

I feel there should be a distinction between "forest canopy" and "tree canopy," where the tree canopy is the aggregate of all tree crowns, and forest canopy is the aggregate of all plant crowns in a forest. The forest canopy, then, includes the mosses and herbs on the forest floor up through the vertical profile of the forest to a point above the uppermost tree crowns where physical factors, such as wind, are no longer influenced by the forest. The entire volume of space, and all the plant structural components as well as biotic organisms within it, from the forest floor on up, could be considered the "canopy" of a forest.

To facilitate information exchange in the world of canopy science, Nadkarni et al. (this issue) have developed the International Canopy Network (ICAN). ICAN maintains a computer network, literature database, newsletter, and catalogue of research scientists working the field of canopy ecology. For those interested in staying current in the field, this is an important group to interact with (2103 Harrison NW, Suite 2612, Olympia, Washington, 98502-2607, USA).

We hope this special issue on Northwest Forest Canopies serves to inform, inspire, and involve more people in the scientific exploration of forest canopies.

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An Overview of Forest Canopy Ecosystem Functions with Reference to Urban and Riparian Systems

Abstract

Functions of forest canopy ecosystems generally include photosynthesis; sexual reproduction of trees; light absorption, modification, and shading; nutrient cycling; atmospheric interaction; hydrologic interaction; and biodiversity. In this paper, we briefly review some of these functions and draw comparisons from two specialized systems, the urban and the riparian. Urban forest canopies abate noise, ameliorate urban temperature increases, conserve energy by shading buildings, and capture particulate matter, pollutants, and carbon dioxide from the air, which makes cities more livable for people. Riparian and wetland forest canopies affect temperature and primary production of aquatic habitat by shading, influence productivity by controlling allochthonous inputs including coarse woody debris, and provide unique habitat for wildlife and other biota.

Introduction

The forest canopy has been called an "independent and complex subsystem" (Carroll 1979) of the forest itself, where a myriad of organisms interact with the trees to effect ecosystem function. The forest canopy is more than a simple collection of tree crowns; it encompasses the living biotic components within these crowns as well as the residues of biota, dead wood, and abiotic components such as atmospheric particulate matter and gases. Forest canopies also "work"; that is they function within the ecosystem, one example being photosynthesis-the conversion of atmospheric carbon and light energy to sugars, a primary product on which most of life on Earth depends. Until recently, forest canopies have received little detailed attention because of the obvious difficulties of access. New technologies that afford access to the canopy (Moffett and Lowman 1995) are helping improve our knowledge of this complex subsystem and thus foster a more holistic understanding of forest ecosystems.

The functioning of forest canopies is important to the forest ecosystem as a whole. Processes of individual tree crowns extend to and from the roots, from the roots to the soil, and throughout the forest floor. Ecosystem functions of forest canopies include photosynthesis; sexual reproduction; light absorption, modification and shading; nutrient cycling; atmospheric-meteorological interaction; hydrologic interactions; and biological diversity. In this paper, we provide a brief overview of these general functions of forest canopies, followed by a discussion of two unique ecosystems—urban and riparian/wetland forests—that we believe deserve special reference.

Ecosystem Functions

Photosynthesis is the primary function of forest canopies (Holbrook and Lund 1995). Carbohydrates produced by the chemical fixation of carbon dioxide in the presence of light become the energetic basis of most forms of life. Within forest ecosystems, net primary productivity is controlled by the rate of photosynthesis and respiration in the canopy, and the allocation of the photosynthate to wood, respiration, and metabolic maintenance costs of other tissues and symbiotic organisms (Waring and Schlesinger 1985). The process of photosynthesis in leaves, controls material transfers of water, carbon dioxide, and pollutant uptake between the forest canopy and the atmosphere. Thus, understanding photosynthesis at the scale of forest canopies provides insight into productivity of forests, forest health, and nutrient and carbon cycling, from local to global scales.

Sexual reproduction of trees occurs in the forest canopy. Growth and development of flowers and cones, meiosis, genetic recombination, pollination, fertilization, maturation of fruit and cones, all occur in the canopy. Therefore, the basic processes which control evolution and the success of tree species is dependant on canopy ecology.

Forest canopies absorb and modify light, and shade the forest floor. The composition and structure of the forest canopy influences these features

(Canham et al. 1990, Canham et al. 1994, Parker 1995), which has implications for growth and productivity of understory plants, within-canopy photosynthesis, plant morphogenesis, and communication between animals and between plants and animals (Endler 1993). Shading influences the temperature of the forest floor and the soil, which controls the activity rates of soil microflora and fauna and of decomposition and nutrient cycling.

The physical and biological features of forest canopies play an important role in the cycling of nutrients. The canopy is a complex structure that provides a surface for wet, dry and cloud water deposition of mineral nutrients from the atmosphere, and the type of structure can influence the rate of deposition (Lovett 1994). The biotic features of the forest canopy function to capture, transform, and cycle nutrients within the canopy as a complex and independent subsystem of the whole forest (Carroll 1979, Edmonds et al. 1991, Coxson and Nadkarni 1995). Carroll (1979) has described complex trophic structures in forest canopies in Douglas-fir forests of the Cascade Range in Oregon, based on studies of the flow of nitrogen. Nitrogen enters the subsystem via atmospheric deposition, transport from the soil, and fixation in the canopy by cyano-lichens such as *Lobaria oregana*. Micro-epiphytic fungi, yeasts, and bacteria on the surfaces of leaves and twigs absorb and concentrate nitrogen deposited from the atmosphere or leached by cyano-lichens. These micro-epiphytes are then grazed by mites and other invertebrates, which are then consumed by a host of predators. Preditors in the canopy also consume the herbivores. The resulting trophic structure, similar to that in streams or other ecosystems, acts to conserve nutrients and enhance productivity of the forest.

Coxson and Nadkarni (1995) have reviewed the role of epiphytes in nutrient cycling of forest canopies. They list five reasons that canopy epiphytes and other biota can be important components of ecosystem function:

1) pools of nutrients and organic matter generated by epiphytes contained in the canopy can be high, even exceeding host tree foliage;
2) the contribution of epiphytes to complex canopy structure may enhance wet and dry deposition by increasing the physical area of canopy surfaces for impaction and sedimentation, and by increasing the biotic uptake by nutrient-efficient epiphytic plants;
3) free-living and symbiotic biota in the canopy can fix atmospheric nitrogen;
4) certain microbial activities (e.g. nitrification) in the canopy appear to be suppressed, relative to the forest floor, which tends to foster nutrients in a form that is less mobile and leachable; and
5) pools of canopy held nutrients are by no means static: nutrients move from the canopy to the other ecosystem members by four routes: a) as litterfall via abscission and by "riding down" fallen branches and whole trees, which is subsequently mineralized at variable rates, b) as crownwash in the form of throughfall and stemflow; c) via herbivory and predation of epiphytes by vertebrates and invertebrates, and d) directly to host trees via uptake by canopy roots.

The canopy component of forests plays an important role in the hydrologic cycle as the primary surface for interaction with rain, fog, and snow. In the Pacific Northwest, where trees grow large, the canopy of a Douglas-fir/western hemlock forest *(Pseudotsuga menziesii/Tsuga heterophylla)* may hold 3 x 10^6 liters/ha of water (equivalent to 3 cm of precipitation) (Franklin et al. 1981), and summer throughfall averages 76% of gross precipitation (Rothacher 1963). Much of the water captured by the canopy returns directly to the atmosphere through evaporation, soil water reaches the atmosphere through transpiration. Fog drip, caused by condensation of wind-driven clouds on conifers can be significant in some montane forests. Harr (1982) found that gross precipitation was greater in forests of the Bull Run Watershed in the Cascade Range of Oregon than clearcuts because of this condensation, and the cutting of the forests resulted in lower streamflow.

A major function of canopies in areas of high snowfall is the interception and storage of snow and the release of snow as meltwater or water vapor (Harr 1986, Berris and Harr 1987). In the transient snow zone, where rain-on-snow events are common, coniferous forest canopies appear to reduce the peak flows of stream water compared to clearcut areas and function as a buffer for the ecosystem, reducing extremes of water release and

the erosion associated with them (Harr 1986, Berris and Harr 1987).

The forest canopy is a porous, living, medium that constantly interacts with the atmosphere, exchanging water, energy, and carbondioxide and other gases, while absorbing wind energy, heat, and radiation (Nadkarni 1994, Fitzjarrald and Moore 1995, Parker 1995). Waring and Schlesinger (1985) estimate that "the equivalent of the entire atmospheric content of carbondioxide passes through the terrestrial biota every 7 years, with about 70% of the exchange occurring through the forest ecosystems." These interactions between canopies and the atmosphere influence microclimate in the forest stand, as well as local, regional, and global climate. The structure and composition of the forest canopy controls the magnitude of atmospheric interaction (Parker 1995).

Forest canopies control biological diversity by physically dominating the potential substrates and resources of the aboveground system, contributing litter and woody debris to the forest floor, and providing photosynthate that fuels the belowground system. Biological diversity in the canopy (and elsewhere) is influenced by forest canopy age, composition, and structure, particularly in the coniferous forests of the Pacific Northwest (Franklin et al. 1981). Epiphytes in Douglas-fir/western hemlock forests, for example, appear to reach highest biomass and diversity in old-growth forests, partly because the deep, vertically stratified canopy has more complex and heterogenous microclimatic conditions than younger, even-aged forests (McCune 1993, Sillett and Neitlich this issue). Wood decay and associated micro-organisms reach their greatest abundance in old-growth canopies (Parks and Shaw this issue). Microfungi act as parasites, symbionts, and microepiphytes, the diversity of which reflect the diversity of potential substrates (Stone et al. this issue). Invertebrates, especially arthropods, have more complex food webs and higher species diverisity in older canopies (Winchester and Ring this issue). Vertebrates, such as arboreal mammals (Carey this issue), bats (Wunder and Carey this issue), and birds (Sharpe this issue), find more diverse resources in older canopies than in young, even-aged canopies.

Specialized Canopy Ecosystem Functions

In the Pacific Northwest, we recognize two distinct ecosystems in which forest canopies have functions unique from the typical terrestrial canopies: urban and riparian/wetland. For example, shade is a function of canopies in all these ecosystems, but the effects of shading are different. In urban areas, the canopy shades built surfaces, resulting in less heat absorption and re-radiation, and thus cools the environment and ameliorates the heat sink effect by which urban areas contribute to global warming. In riparian forests, shade controls primary productivity in streams and the temperature of water, which has a direct influence on fish production (Franklin et al. 1981). In terrestrial environments, shade from the forest canopy directly controls the productivity of the plants on the forest floor, which influences populations of herbivores.

Urban Forest Canopies

Because of a growing human population and expanding urban areas, urban forests are increasingly important both locally in the Pacific Northwest and globally. For example, an estimated size of the potential urban forest, as the current area of incorporated cities and towns, in a four-county area of western Washington (Whatcom, Skagit, Snohomish, King), is 166,281 ha (649 square miles). One hundred and fifty years ago, this same area was relatively pristine. The urban forest is unique compositionally. For example, Seattle has more than 740 species and varieties of trees in the urban area, but the original vegetation had only about 29 species (Jacobson 1989). The extreme diversity of trees in the urban area gives urban planners and designers a plethora of options in integrating trees into the urban environment, and in a sense, engineering ecosystem functions of the urban forest.

The urban environment/ecosystem is particularly important because of the direct influence on human physical comfort, health, and use of energy resources (Rowntree 1986, McPherson and Rowntree 1993, Nowak 1993). Urban forest canopies (Figure 1) act to abate noise (Mecklenberg et al. 1972, Reethof and Heisler 1976, Mao et al. 1993); check atmospheric contaminants (Smith and Docincher 1976); shade built surfaces, which reduces the amount of radiant energy absorbed, stored, and radiated (McPherson and Rowntree 1993); modify microclimate (Federer 1976, Heisler and Herrington 1976, Oke, 1988, 1989, Wilmers 1990/1991, McPherson and Rowntree 1993, Mao et al. 1993); ameliorate the urban heat sink effect;

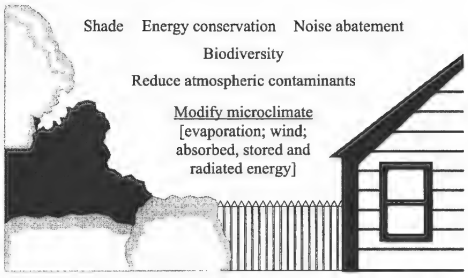

Figure 1. Characteristics of the urban forest canopy.

conserve energy (Heisler 1986, Wilmers 1990/ 1991, McPherson and Rowntree 1993); and influence biological diversity of urban areas (Rowntree 1986).

The modification of microclimate, saving of energy resources, and amelioration of urban heat sink are well-studied ecosystem functions of forest canopies . In addition to the cooling effect of shading, evapotranspiration converts radiant energy into latent energy, which reduces sensible heat that warms the air; air flow modification by urban forest canopies affects transport and diffusion of energy and water vapor. Temperatures in greenspaces of buildings have been shown to be as much as 3 degrees C cooler than adjacent areas outside the greenspace, and temperature differences of more than 5 degrees C have been observed between cities and more-vegetated suburban areas (McPherson and Rowntree 1993).

Riparian/Wetland Forest Canopies

Riparian forests have received considerable attention for their influence on aquatic ecosystems (Salo and Cundy 1987, Raedke 1988, Gregory et al. 1991, MacDonald et al.1991). Within the same four-county area of western Washington viewed for urban areas are 17,697 linear kilometers of mapped streams and rivers (Nooksack, Skagit, Samish, Stillaguamish, Snohomish and the Lake Washington/Cedar River watersheds). The estimation of extent of the riparian forest is complicated and depends in part on the classification of intermittent streams (Swanson et al. 1982, Gregory et al. 1991). To estimate the size of the riparian forest in this four-county area, we have estimated 100 m on either side of the rivers and streams as the riparian forest, which give about 353,934 ha.

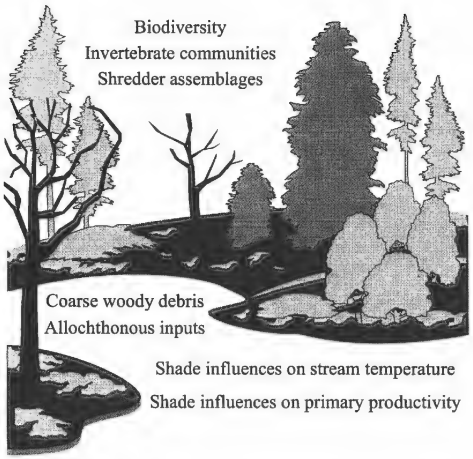

Figure 2. Characteristics of the riparian//wetland forest canopy.

Shade from riparian canopies (Figure 2), and its affect on solar radiation, has a major influence on the aquatic environment (Swanson et al. 1982, Hawkins et al. 1983, Gregory et al. 1991). Shade influences stream temperature, which influences the amount of oxygen in the water, rates of decomposition, and activity of stream animals. Shade also influences primary productivity of aquatic plants, thus affecting net primary productivity of streams (Swanson et al. 1982, Gregory et al. 1991). Direct insolation in small scale openings in streams resulted in a higher density of vertebrates presumably because of increased algae growth, increased grazing insects, and an improved food supply for fish and salamanders (Hawkins et al. 1983).

Allochthonous inputs into aquatic habitats are primarily controlled by the forest canopy. Litter quantity and quality influence communities of invertebrates, such as shredders (Swanson et al. 1982, Cummins et al. 1989) and the food webs they spawn. Coarse woody inputs into stream environments play an important role in the structure of the aquatic environment, creating a complex of pools, backwaters, ripples and eddies (Swanson et al. 1982, Gregory et al. 1991).

As in other ecosystems, the age, structure, and composition of riparian canopies directly influence ecosystem functions (Swanson et al. 1982, Hawkins et al. 1982, 1983, Bilby 1988, Gregory et al. 1991, Bilby and Bisson 1992). Gregory et al. (1991) cite the example of dense, low,

overhanging canopies greatly reducing light, yet high, relatively open canopies allow more light to reach the stream.

Riparian forest canopies contribute to biologic diversity because the composition and structure of these forests is often distinct from adjacent upland forests. Microclimatic conditions associated with flowing water create distinct habitats, and a natural "edge" is created by the continual disturbance to streamside vegetation. Epiphytic communities may be more abundant and have more cyano-lichens (Sillett and Nietlich this issue), and bird communities also respond to the unique vegetation and habitats (Sharpe this issue).

Summary

Canopies form a complex subsystem in forest ecosystems. Organisms such as microbes, fungi, epiphytes, invertebrates, and vertebrates, along with the associated vegetative composition and structure interact to influence ecosystem functions. Urban forests and riparin/wetland areas illustrate the important processes and functions of forest canopies. To link canopy ecosystem functions with the objectives of ecosystem management requires a more integrated research focus on complex canopy interactions across diverse ecosystems than has been used in the past.

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Forest Canopy-Atmosphere Interactions

Abstract

Exchanges of materials (gases, nutrients, water, pollutants, and energy) between forest canopies and the atmosphere drive important ecosystem processes and influence many meteorological phenomena. Trees must exchange water, carbon dioxide, and energy with the atmosphere to survive. As new instruments and quantitative tools emerge for measuring forest and atmospheric conditions, the complexities of canopy-atmosphere interactions can be more accurately understood and modeled. Improved knowledge of canopy-atmosphere interactions is becoming more important as human activities alter both the structure and function of forest canopies, as well as the chemical and physical properties of the atmosphere. The increased scientific focus on structural and functional attributes of forest canopies in recent years promises to yield new insights into the effects of human disturbance on environments in forest canopies and the atmosphere. Important topics for future research in canopy-atmosphere interactions include: (1) the influence of elevation, forest edge, and canopy roughness on atmospheric deposition of pollutants; (2) the dynamics of carbon sequestration in forest biomass in relation to forest management practices and other disturbances; (3) the effects of anthropogenic pollutants on forest functioning and atmospheric feedbacks; and (4) the functional changes in forest canopies associated with structural changes, and consequences for watershed hydrology and nutrient cycling.

Introduction

The forest canopy forms a major interface with the atmosphere over much of Earth's surface. Canopy-mediated exchanges of mass and energy largely define ecosystem productivity. Key interactions between the canopy and the atmosphere are influenced by environmental conditions such as climate, moisture, and nutrient availability (Mooney and Gulmon 1982, Van Cleve et al. 1983). In turn, wind velocity, energy budgets, rainfall, and other environmental conditions are variably modified by the canopy and can affect forest hydrology (Cavelier and Goldstein 1989). Forest canopies modify climates locally, regionally, and globally (Avissar and Pielke 1989, Shukla et al. 1990). Changes in the pool sizes and fluxes of nutrients, water, and carbon through forest ecosystems have important consequences not only for the prosperity of human economic systems, but also for the sustainability of life on Earth.

As a consequence of complex meteorological and biological processes, resources and microclimates within forest canopies are spatially and temporally diverse. Within these canopy "niches," specialized organisms have evolved that alter the environment for other species and iteratively form a trophic chain or "food web." Complexity and diversity at one level nurture complexity and diversity at yet higher levels. This paper explores some of the important interactions between the atmosphere and forest canopies in terms of canopy physiology, function, and structure, with emphasis on coniferous forests. An overview of canopy-atmospheric functions and interactions is provided, including the interception, retention, modification, and conductance of energy (light, heat), gases (primarily carbon dioxide), water, and nutrients (Figure 1). Canopy interactions with wind and pollutants also are briefly discussed.

Anthropogenic disturbances such as deforestation, stratospheric ozone depletion, pollution, biomass burning, water shortages, and other factors associated with expanding human populations and industrialization pose a growing threat to forest ecosystems. A better understanding of interactions between forest canopies and the atmosphere is urgently needed to accurately assess, mitigate, and perhaps prevent negative impacts on ecosystem health from human disturbance.

Trace Gases

Trace gases in the atmosphere range from highly reactive species with lifetimes in seconds to hours, to stable compounds with lifetimes in years or centuries. The sources, sinks, and dynamics of these gases are important for several reasons. First, many gases affect the chemistry and physics of the atmosphere and thereby can affect various natural processes, such as concentrations of tropospheric oxidants, ultraviolet absorption in the stratosphere, and the energy budget of Earth. Second, trace gases or their reaction products inter-

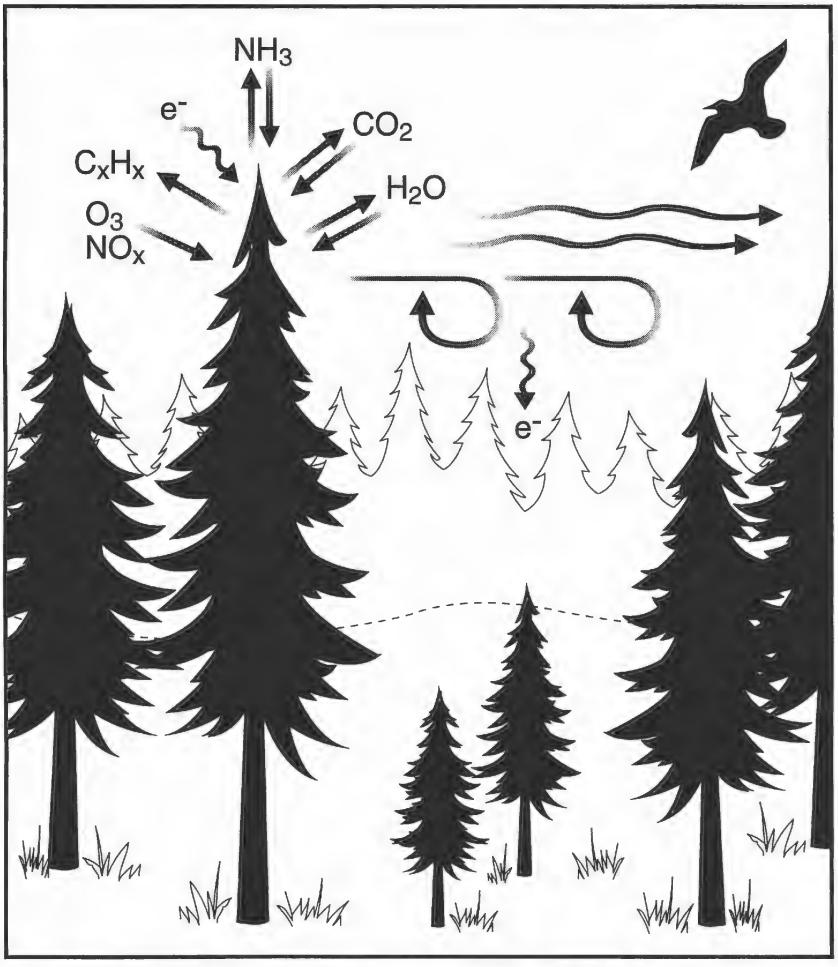

Figure 1. Complex and interacting processes influence the exchange of materials and energy between forest canopies and the atmosphere.

act with the biota to cause a multitude of effects ranging from increased productivity to heavy mortality. Third, the production or consumption of these gases serves as an important indicator of ecosystem functioning. The forest canopy is a major biologic entity interacting with the atmosphere to influence the concentrations and fluxes of trace gases. Consequently, the mechanisms of this interaction are important to understanding the dynamics of terrestrial ecosystems in relation to the atmosphere.

Excluding the anthropogenic chlorofluorocarbons, the more stable gases are generally higher in concentration, and seasonal distribution patterns are better characterized. Long-term trends in concentrations have been documented in ice bubbles from Antarctic ice cores (Rasmussen and Khalil 1984, Pearman et al. 1986). This group of gases includes carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O), three stable biogenic gases that are increasing globally.

Carbon Dioxide

Energy to drive most processes in forest ecosystems is derived initially by the fixation of atmospheric CO_2 into sugars through photosynthesis

in leaves. In photosynthesis, CO_2 diffuses through small pores or stomates, into foliage where it is biochemically reduced to sugars using energy in the form of adenosine triphosphate (ATP) produced by the capture of sunlight by leaf pigments. In respiration, the breakdown of sugars to yield energy for plant growth and metabolism produces CO_2 as an end product. Respired CO_2 then diffuses back out of the leaf stomates into the atmosphere.

The uptake of CO_2 by forest ecosystems during the daytime is controlled primarily by the response of photosynthetic rate to increasing light (photosynthetically active photon flux density, or PPFD) (Hollinger et al. 1994b). The saturating response of leaf photosynthesis to light is explained by the fact that carbon uptake is limited at low PPFD by insufficient electron transport and photophosphorylation, and at high PPFD by insufficient carboxylation capacity (Farquhar et al. 1980, Kirchbaum and Farquhar 1984). In response to temperature, photosynthesis in many species has been found to reach a maximum between 15 - 30 °C. This results from the differential effect of temperature on the kinetics of RuP_2 carboxylase-oxygenase for carbon dioxide and oxygen (Berry and Raison 1981). Other factors such as vapor pressure saturation deficit and water stress also can directly inhibit photosynthetic mechanisms, and indirectly inhibit photosynthesis by reducing stomatal aperture (Morison 1987). Similarly, the functional response of nighttime respiration to temperature dominates the production of carbon dioxide by leaves. Respiration during darkness increases approximately exponentially with the inverse of the absolute temperature.

Forest canopies differ in their productive capacities and their rates of exchange seasonally and in relation to temperature and the availablility of water and nutrients. For example, humid tropical forests comprise only 6.6 percent of Earth's surface area, but accomplish 17 percent of the total net primary production. Another generalization is that young forests are a more efficient sink for CO_2; however, older forests contain larger stores of carbon.

A recent study by Hollinger et al. (1994b) explored how environmental modifications by a forest canopy potentially alter basic patterns of ecosystem CO_2 exchange compared to the current understanding of leaf gas exchange. Net flux between the ecosystem and the atmosphere was determined from the sum of the eddy flux above the forest and the change in the mean concentration of CO_2 in the forest air below the canopy. The CO_2 exchange patterns were similar in many ways to patterns observed at the leaf level. Seasonal changes in the relation of CO_2 uptake and dark respiration varied however, with other environmental and physical characteristics that had little importance at the leaf level, such as the above-canopy spatial distribution of PPFD and turbulent transport.

This and other recent studies have demonstrated that in modeling CO_2 exchange, forest canopies cannot be treated as simple analogs of leaves. At the canopy level, gas exchange is controlled not only by biological processes in the leaf, but also by canopy architecture, temporal changes in the environment, site characteristics, and environmental gradients that vary spatially around vegetation (Norman 1993). Modeling efforts that attempt to scale atmospheric interactions to the level of whole canopies are described by Baldocchi (1993), Norman (1993), and Schimel et al. (1993). Modeling of gas exchange in conifer canopies is described by Price and Black (1990) and Wang and Jarvis (1990).

Approaches to modeling whole-canopy photosynthesis are reviewed by Norman (1993). The most popular approaches to estimating canopy gas exchange use the following variables: (1) absorbed, photosynthetically active radiation and leaf photosynthetic efficiency; (2) average illumination and leaf area index; (3) photosynthetic rate and total leaf area; (4) photosynthetic rate and leaf area of sun and shade foliage; and (5) leaf energy balance and environmental gradients. Particularly important research topics in canopy gas exchange include dynamic variations in turbulence and physiology.

Methane

Tropospheric methane is increasing at about 1.1 percent per year, a substantially greater percentage increase than for CO_2. Methane is produced by specialized anaerobic bacteria that reduce CO_2. Primary sources of methane include anaerobic environments, such as wetlands, digestive systems of cattle and termites, and mining of fossil fuels (Mooney et al. 1987). Methane may have an indirect effect on forest canopies through its

influence on climate and atmospheric chemistry. A strong greenhouse gas, methane absorbs outgoing infrared radiation within the troposphere 20 times more effectively per molecule than does CO_2. In addition, by reacting with hydroxyl radicals, methane can produce compounds harmful to canopy foliage, such as carbon monoxide (CO) and ozone (O_3).

Nitrogen

Although dinitrogen (N_2) is the most abundant element in the atmosphere, it is also the element that most limits photosynthesis and primary production in many terrestrial ecosystems. This paradox is explained by the fact that N_2 in the atmosphere can be converted to biologically available forms by only a few species of prokaryotes, and because the process of nitrogen fixation is energetically expensive. Forest canopies are important sources of nitrogen fixation by both free-living and symbiotic bacteria on vegetation and epiphytes. Another form of nitrogen, nitrous oxide, N_2O, is increasing globally due primarily to combustion. Nitrous oxide may affect forest canopies by contributing a small amount towards the breakdown of the stratospheric ozone layer and to global warming in the next several decades (Mooney et al. 1987).

Reactive Gases

Reactive gases are produced biologically and by combustion, but are more difficult to quantify due to their ephemeral nature. The effects of these gases also are problematic because they can interact regionally or locally to cause the production or destruction of other gases having a major impact on atmospheric chemistry and terrestrial biota. Major classes of reactive gases include the non-methane hydrocarbons (NMHC) and CO. The NMHC, including isoprene and terpenes, are linked to the destruction of ozone and production of atmospheric CO. There is no evidence, however, that atmospheric concentrations of NMHC directly affect physiological or biochemical characteristics of foliage. Carbon monoxide has no direct biological effects at current atmospheric concentrations, but it interacts with nitrogen oxides and hydroxyl to produce tropospheric ozone, a phytotoxic compound.

Reactive nitrogen gases include oxides of nitrogen (N), referred to as NO_X, which are derived primarily from combustion and, to a lesser extent, from biological processes of nitrification and denitrification in soils. The role of NO_x in atmospheric chemistry is complex - under varying conditions, it can catalyze both the production and destruction of ozone. It also is readily converted to nitric acid that forms a major component of acid precipitation downwind of industrial areas. As a fertilizer, N deposition to N-deficient forests may increase plant productivity or stimulate unhealthy changes in vegetation growth patterns and nutrition (Aber and Melillo 1991).

Although present in the atmosphere at low concentrations, ammonia sources have been augmented by intensive agriculture and livestock farming. Atmospheric ammonia can be dissolved or adsorbed by aerosols or precipitation, or be taken up directly by vegetation. In aerosols or cloud droplets, ammonia can protonate to reduce the acidity of precipitation. But if depositied ammonium is retained by vegetation or lost as nitrate, soil acidification results (Binkley and Richter 1987).

Natural terrestrial ecosystems emit an even wider array of sulfur compounds, mostly in anaerobic conditions, including hydrogen sulfide (H_2S), dimethyl sulfide, methyl mercaptan, carbon disulfide, and carbonyl sulfide. All but the last compound are short lived. According to current evidence, the flux of H_2S is much higher in tropical than temperate forests. Sulfur from anthropogenic fuel combustion contributes to acidified precipitation and altered nutrient cycling in forests.

Ozone in the troposphere is a strong oxidant formed by a complex set of reactions involving NO_x gases, hydrocarbons, oxygen, and sunlight. Ozone can injure tree canopies by damaging leaf membranes and inhibiting photosynthesis (Bytnerowicz and Grulke 1992). In fact, on a regional scale, ozone is the only air pollutant known to be phytotoxic at ambient levels in western North America. The literature on ozone effects on forested ecosystems in the western United States is synthesized in Olson et al. (1992). Ozone monitoring data for the Pacific Northwest have been summarized by Eilers et al. (1994).

Radiation and Heat

Radiation absorption in the atmosphere is a function of the pathlength through the atmosphere and the content of absorbing compounds, particularly water

vapor. In addition to shortwave radiation from the sun and sky, an important contribution to the radiation balance of canopies is made by longwave radiation. Longwave radiation is emitted by the gases (especially water vapor and CO_2) present in the lower atmosphere. The presence of clouds increases the downward flux of longwave radiation because clouds are more effective emitters. Radiation losses from the forest canopy include thermal radiation emitted, as well as any incident radiation that is reflected or transmitted (Jones 1992).

Photosynthetic pigments in the forest canopy absorb incident light radiation mainly in the visible wavelengths (Salisbury and Ross 1985). Flux density of radiation in a canopy at a given wavelength is the sum of the direct beam and diffuse sky radiation that penetrates foliage gaps and is modified by scattering on leaf surfaces. Consequently, properties of light at any point in a canopy are dependent on conditions in the atmosphere, and the physical, chemical, and structural attributes of the canopy (Baldocchi 1993). Detailed information on physical attributes of the canopy is needed to assess the diffusive source-sink gradient and the transmission of radiation directly. The total leaf area of a canopy, species compositions, leaf spatial and elevational distribution, and angular orientation all affect the radiation environment of forest canopies. Various stresses to vegetation, including nitrogen deficiencies and moisture deficit, can affect the light absorption and reflectance properties of foliage due to changes in cellular structure and pigment functioning of foliage.

A useful approximation of radiation behavior in forest canopies is that a constant fraction is absorbed per unit distance into the canopy. This produces exponential light decay with increasing cumulative leaf area. The decay of radiative energy with distance into the canopy causes heating of the biomass and air that produces a stable density stratification in the canopy of warmer lighter air above, and cooler denser air below and partially isolates the lower canopy from the atmosphere. This effect is strongest for canopies with thick foliage near the top. At night, the canopy interferes with the loss of longwave radiation under the canopy, whereas substantial radiative cooling occurs above the canopy, and leads to strong stable layers near the top of the canopy. Temperature and humidity at the leaf surface are determined by the balance of incoming shortwave and longwave radiation and its partitioning into sensible and latent heat exchange. When considering energy partitioning of the whole canopy, advection, and soil and canopy heat storage also must be taken into account (Baldocchi 1993). Important to note too, is that heat transport in forests can move up the gradient, contrary to expectations. This is because sporadic turbulence at scales much larger than the local gradient can produce "up-gradient" mixing.

Water

Less than 1 percent of Earth's water is contained in the atmosphere, soil, lakes, and rivers. The atmosphere contains only 0.001 percent of Earth's water, which would amount to an average depth over the planet's surface of 20-30 mm (Mooney et al. 1987). Nevertheless, water is an important controlling factor in vegetation processes and in tropospheric temperature structure through effects on both solar and terrestrial radiation.

Water vapor transfer depends on the flows of energy that convert liquid to vapor and on molecular and turbulent diffusion that transfers water vapor molecules between the leaf and the free air. As with CO_2 exchange, water vapor exchange from tree canopies is dependent on all biological and structural attributes that influence local concentrations in the canopy, such as radiation, temperature, turbulence, humidity, and leaf physiological condition.

Actual evapotranspiration (AET) is the sum of all water lost to the atmosphere from the soil or vegetation surfaces (evaporation) and through plant tissues (transpiration). Potential evapotranspiration (PET) is the amount of evapotranspiration that would occur with unlimited water supply. In drier climates, AET is lower than PET. Evapotranspiration increases directly with water availability and with higher evaporative demand at the leaf surface (higher temperature and lower humidity) (Aber and Melillo 1991).

Forest canopies interact both directly and indirectly with the hydrologic cycle. Leaves, branches, and stems intercept and redirect water to the soil in throughfall or back to the atmosphere via evaporation and transpiration. Annually, as much as a third of the incoming precipitation may be intercepted by forest canopies ranging from tropical to boreal types. Structural aspects of the canopy influence the amount of intercepted ra-

diation, boundary-layer characteristics, and the amount of water available for evaporation. These influences are evident when forest cover over an entire watershed is removed and streamflow increases substantially.

Water movement from the soil through the forest canopy to the atmosphere is driven by a series of interrelated, interdependent proceses. For example, the rate of water absorption by the soil is affected both by the rate of water loss from the leaves to the atmosphere and by the rate at which water can move from the soil to the root surface. Water loss and interception by tree canopies also is influenced by both the amount and duration of leaf area. For example, pine forests lose more water to the atmosphere than do hardwoods, owing to higher leaf area and to the maintenance of needles year-round. Species-specific differences in water loss also exist. Species with deep roots that can access abundant water supplies, typically sustain higher rates of evapotranspiration (Waring and Schlesinger 1985).

The quantity and distribution of water vapor controls both ecosystem and atmospheric dynamics directly. Changes in Earth's energy balance in response to greenhouse warming are expected to dramatically alter regional water budgets (Mooney et al. 1987). Hollinger et al. (1994a) recently found rapid transmittance of hydraulic pulses from the top of a Nothofagus tree to a mid stem and basal stem position, respectively. These pulses were induced by changes in atmospheric humidity as air of various moisture content passed over the canopy. These findings indicate that the water column is under tension governed by physical forces and that water storage plays little role. Additional research is needed to clarify the mechanisms governing evapotranspiration by forest canopies.

Nutrients

The forest canopy is a major repository of plant and ecosystem nutrient capital. Processes within the canopy influence the retention, uptake, leaching, and redistribution of nutrients within the canopy and among the canopy, the soil, and the atmosphere. In addition to the uptake of nutrients depositied in various forms from the atmosphere to the forest canopy, canopies also are emitters of various compounds, including hydrogen sulfide, ammonia, and K-, S-, and P-containing aerosols. During fires, large quantities of nutrients also are lost in the gases and smoke from forest canopies (Waring and Schlesinger 1985).

Ecosystem carbon and nutrient cycles are mutually linked because the chemical composition and quantity of litter supplied by the canopy modulate the processes of decomposition, mineralization, and nitrification (Fogel and Cromack 1977, Meentemeyer 1978, Melillo et al. 1982, Pastor and Post 1986). Canopy-atmosphere interactions influence these processes through changes in the carbon and nutrient ratios of foliage mediated by differences in the availability of photosynthate and nutrients. Atmospheric conditions favorable to photosynthesis may increase the foliar carbon-nutrient ratio, whereas conditions limiting gas exchange would have the opposite effect, depending also on site nutrient availability. Furthermore, the canopy influences nutrient cycling by altering moisture and temperature conditions at the forest floor.

Wind and Turbulence

Air in the lower atmosphere is never completely still. There is usually a net horizontal motion or wind, with random movements of smaller air pockets. In free convection, air movements are caused by changes in air density, as results from heating or cooling. In forced convection, air movement is determined by an external pressure gradient causing wind. Forced convection may lead to the generation of eddies or turbulence as a result of frictional forces that develop as wind flows over an object. Characteristics of the eddies and turbulence over a forest canopy combined with attributes of the canopy boundary layer, control many aspects of mass and energy exchange with the atmosphere.

Turbulent motion has a controlling influence on the distribution and redistribution of mass and energy through forest ecosystems. Many aspects of canopy-atmosphere interactions are influenced by the fact that windflows and turbulent exchanges above forest canopies are poorly described by flat-plane boundary layer models. In addition, physical and biological influences on canopy microclimate are often complementary. For example, seed and pollen dispersal depend on a turbulent wind field, which in turn is affected by the biomass profile. Diurnal changes in canopy relative humidity affect the movements of insects and other

organisms. (Murlis et al. 1992, Fitzjarrald and Moore 1995).

Consistent with mean wind profiles, turbulent transport of horizontal momentum decays rapidly below the canopy surface; however, the degree to which the canopy is coupled to the atmosphere changes diurnally, with stronger coupling during the day than night (Fitzjarrald et al. 1988). The term "forest anomaly" has been used to describe the fact that flux profiles above rough forests are not the same as those above flat surfaces (Raupach 1979). This seems to result because the eddies are much larger than their height above the canopy, compared to turbulent flows over flat surfaces. Momentum transport to a canopy depends to a large degree on the roughness of the surface. When canopies are sparse, each tree is considered a roughness element.

Pollutant Deposition

The processes controlling pollution deposition to forest canopies deserve special mention here. Atmospheric deposition occurs through three separate processes: (1) wet deposition in precipitation; (2) dry deposition in particles and gases; and (3) cloud deposition in droplets. Wet and dry deposition are ubiquitous, whereas cloud deposition is common in coastal and mountainous areas. Wet deposition is generally controlled by the concentration, size, and solubility of particles or gases, gas reactivity, and the meteorological processes affecting precipitation. Dry deposition is controlled by many factors, including atmospheric chemistry and meteorology; canopy structure; and physiological, chemical, and structural properties of foliage. Cloud-fog deposition is controlled by factors similar to wet deposition, though properties of the receptor surface are more important (Lovett 1994).

Coniferous forests with fine needles are highly efficient at collecting wind-driven cloud droplets (Unsworth and Wilshaw 1989). Previously deposited pollutants on leaf surfaces can dissolve, creating more concentrated solutions than the incident cloudwater. Furthermore, moistened leaf surfaces increase deposition of particles by reducing bounce-off and resuspension, and by providing a sink for soluble gases. Diffusion through stomates is a primary pathway for entry of gases into leaves. Gases also may react chemically with leaf surfaces and remain fixed. Deposition rates for gases are thereby affected by both stomatal response and environmental effects on stomatal conductance. Stomatal closure during summer drought may afford some protection from ozone during this period. Dry deposition via minute particles is negligible, although fine sulfate particles may enter stomates.

Properties of the plant cuticle determine the interactions with wet deposition. Precipitation may be both a source and a sink for pollutants. As polluted water evaporates from the leaf surface, ion exchange may occur between the leaf interior and surface. With rapid evaporation, acid may reach damaging levels on leaf surfaces. Soluble gases also may diffuse into the water film. The most important canopy transformations of incident precipitation are the direct assimilation of nutrients by foliage, hydrogen ion buffering in the canopy, and metal cation leaching (Bredemeier 1989).

Although beyond the scope of this paper, atmospheric processes have important effects on the transport and dispersion of atmospheric pollutants. These processes have major consequences for regional patterns of pollutant deposition in mountainous areas. See Bôhm (1992) for a review of regional deposition in relation to atmospheric processes.

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Analyzing Canopy Structure in Pacific Northwest Old-Growth Forests with a Stand-Scale Crown Model

Abstract

In forests, the canopy is the locale of critical ecosystem processes such as photosynthesis and evapotranspiration, and it provides essential habitat for a highly diverse array of animals, plants, and other organisms. Despite its importance, the structure of the canopy as a whole has had little quantitative study because limited access makes quantification difficult and integration of detailed measures of many individual tree crowns is necessary. A model is presented for simulating the crown architecture of individual trees in the Pacific Northwest to analyze their collective influence on canopy structure at the stand scale. The model uses ground-based measurements of tree height, height to crown base, and crown radii. Crown shapes are modeled as solid geometric shapes based on these measures. Two examples are used to illustrate the model's applications: an estimation of the vertical distribution of foliage in an old-growth Douglas-fir/western hemlock forest; and an estimation of understory light conditions in an experimental gap, made by applying ray tracing technology to a model of the overstory tree crowns. Both examples illustrate how the model can increase detail in the description of canopy structure. Further application and future testing of the model will help refine its precision.

Introduction

The forest canopy has been hailed as one of the last biological frontiers and the greatest source of species diversity in forests (Erwin 1982, Schowalter 1988, Lesica and Antibus 1991, Terbough 1985, 1992, Wilson 1992). Canopies are critical elements of the forest ecosystem from numerous viewpoints. They modify both meso- and micro-climate, affect regional evaporation, cloud condensation, and temperature fluctuations (McNaughton 1989, Harr 1982, Chen 1991). The canopy is the exchange site for atmospheric gases, precipitation, and particulate interception (Hutchinson et al. 1986, Campbell and Norman 1989, Gao and Li 1993). In old-growth forests of the Pacific Northwest, the complex canopy structure has been recognized as essential for many species of wildlife, arthropods, and epiphytes (several articles, this issue). Research in forest canopies has been limited, however, by both the logistical problems of accessing the tall tree crowns, and the heterogeneous structure of the canopy environment. Despite numerous studies of canopy processes and species diversity, the structure of the canopy remains poorly understood and has rarely been quantitatively analyzed.

Other studies of canopy structure have examined the fine scale of individual tree crown architecture (Massman 1982) or large-scale canopy cover for a watershed or landscape (Cohen and Spies 1992, Wu and Strahler 1994). Detailed measures of branch patterns and leaf orientation can be used to assess shade tolerance or branch architecture (Hutchinson et al. 1986, Canham 1988), but these measures are specific to the structure of individual trees or the canopy process under study (Norman and Campbell 1989). Aerial photography and satellite imagery are used to examine changes in canopy cover with succession or disturbance (Cohen et al. 1990, Nel et al. 1994, Nilson and Peterson 1994), but they do not provide detailed information on the internal structure of the canopy.

Measures of canopy structure at intermediate spatial scales are not well developed because stand-scale analysis requires direct measurement of many tall, complex tree crowns. In mature and old-growth forests, accessing and measuring a sufficient sample of tree crowns to describe a stand's canopy structure is difficult. In spite of these difficulties, a three-dimensional stand-scale measure of canopy structure is needed for at least three reasons: this scale is necessary to link processes operating across fine (individual tree architecture) and coarse (remote measures of large-scale canopy cover) scales of structure; many arboreal wildlife species may respond to canopy structure at this scale; and land management monitoring and planning often occur at the stand scale.

A direct method of modeling the canopy structure of old-growth forest stands in the Pacific

Northwest is presented in this paper. The model is used to quantitatively describe the vertical distribution of crown foliage within a stand and associated effects on the amount of light in the understory. Estimates of individual crown volumes are made from ground-based measures of tree height, height to the live crown, crown shape, and crown diameter. Although these methods were developed in coniferous old-growth forests, the techniques should be applicable to other forest types, to successional stages where canopy structure may be less complex, or both. As research activities in forest canopies increase, standardized methods for quantitatively analyzing canopy structure are needed. This model is presented as a preliminary approach toward measuring stand-scale canopy structure while the model's accuracy is tested further.

Approaches to Measuring Canopy Structure

Canopy Structure and Tree Age

Canopy structure refers to the spatial arrangement of tree stems, branches and foliage within a forest. As forest stands develop, the vertical and horizontal distribution of the canopy becomes more heterogeneous, and its measurement becomes more difficult. In young stands of trees, particularly conifers, canopy structure is fairly homogeneous and growth patterns are predictable. Models of individual trees can predict annual branching patterns, branch angles, and leader and branch extension lengths with some accuracy for young trees (Hamilton 1969, Horn 1971, Hatch et al. 1975, Halle et al. 1978). Growth and yield models, such as OREGANON (Hann et al. 1992), can provide good estimates of a tree's crown growth, including responses to thinning mortality.

As trees age, however, they become taller and their crowns longer, more complex, and more idiosyncratic. Trees in an old-growth forest are products of hundreds of years of individual responses to disturbance, competition, injury, light availability and quality, and other stochastic events. For each tree, the sum of these collective differences creates a unique, complex, crown shape that is difficult to predict or model (Canham 1988, Young and Hubbell 1991). In conifer forests, the canopy may begin as a fairly uniform band of cone-shaped crowns, and develop into a multilayered array of polymorphous crown shapes. Maps of the foliage distribution in individual old-growth Douglas-fir trees at the H.J. Andrews Experimental Forest in central Oregon showed that the crown shape of each tree was unique and irregular (Pike et al. 1977, Massman 1982).

Scale and Access

Canopies are studied at many different scales depending on the arboreal species or process. From landscapes to stands to individual trees to branches, the scale of interest determines the detail at which canopy structure should be measured (Kruijt 1989). Researchers interested in fine-scale processes are not concerned with the unique shape of each old-growth tree crown. When canopy-dwelling arthropods are being studied, for example, foliage distribution on a single branch can be examined for habitat use and availability (Winchester, this issue). For studies of photosynthesis and particulate interception, canopy structure may require a map of foliage or branch distribution within a single crown. When working at these scales, direct access to the canopy is possible using towers, lifts, or rope techniques developed by urban arborists. Athough these systems are time consuming to establish, they afford precise measurments of crown components.

Landscape ecologists and foresters interested in canopy structure on a watershed or regional scale rely on remote imagery from airplanes and satellites (Woodcock et al. 1990, Wu and Strahler 1994). Remote methods eliminate access problems and increase the canopy sample size, but also decrease detail. Digital satellite imagery has been used to classify forest stands by age class across landscapes, by using the reflectance signal of canopies, (Morrison 1989). Digital imagery or videography from low-flying aircraft can distinguish individual tree crowns, shadows and the openness of a stand (Cohen et al. 1990).

Remote imagery provides valuable large-scale images of changes in canopy structure with age or disturbance, but it provides little information about the interior canopy environment. In forests with multiple crown layers, high foliage densities, or irregular crown cover, measures of only the outer canopy surface provide little information about canopy structure. Assessing canopy structure at the stand scale requires integration of numerous measures of individual tree architecture. Measurements must include more than a

sample of a few tree crowns, but must provide greater detail than can be obtained from a remote image of the canopy's upper surface. This compromise between sample size and detail, along with problems accessing mature forest canopies, has often led to the use of indirect measures of canopy structure, such as light transmission.

The amount of light in a forest is influenced by the density and distribution of canopy foliage (Anderson 1963, Horn 1971, Reifsnyder et al. 1971). The percentage of full sunlight that reaches the forest floor is a broad measure of foliage density. The most common methods of measuring light penetration, however, integrate the incoming light over the whole sky (Reifsnyder et al. 1971, Hutchinson et al. 1980, Oberbauer et al. 1988, Chazdon and Pearcy 1991) providing little information regarding the distribution of light as a function of canopy structure. Fisheye photographs can help isolate the direction of incoming light (Evans and Coombe 1959, Anderson, 1963, Horn 1971, Canham et al. 1990); however, each photo represents only a single location, making stand-scale analysis difficult. A larger scale measure of canopy structure that does not use light transmission is leaf area index (LAI), a measure of the number of foliage layers over a given area of forest floor, provides a stand-level index of foliage quantities (Waring et al. 1982). All of these techniques, however, provide little detailed information on canopy structure because they do not measure how foliage is spatially distributed (Oker-Blom and Kellomaki 1982, Chason et al. 1991).

Canopy Structure in Pacific Northwest Old-Growth Forests

Pacific Northwest old-growth forests have tall, multilayered canopies, which are difficult to access and structurally complex. Much of the old growth below 1000 m in elevation is dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*). These forests can be up to 80 m tall, with foliage distributed throughout (Franklin and Waring 1980), so that the amount of understory light provides little information about foliage distribution in the canopy. The trees may be tall but are generally not very wide. Branch lengths seldom exceed 8 m and the upper canopy tends to have distinct crowns because of branch abrasion.

To confound matters, the amount of light reaching the forest floor may not reflect the canopy structure directly overhead. In the Pacific Northwest (at latitudes from 44 to 58°), sun angles are oblique during most of the growing season. Analyses of fisheye photos reveal that significant amounts of light filter through a Pacific Northwest forest canopy at 45 degrees or more off vertical (Figure 1a and 1b) (Easter and Spies 1994). Flat projections of tree crowns used to model canopy effects on understory light may work well in low-latitude tropical forests or short-stature, broadleaf temperate forests (e.g., Runkle 1992), but they do poorly in the Pacific Northwest.

For Pacific Northwest old-growth forests, measurement of the location and crown dimensions of individual trees can be integrated to provide a stand-scale description of canopy structure. Ground-based measurement is a practical compromise between direct measurements of a few branches and remote, large-scale sampling of a forest's outer canopy cover. With ground-based measures, an observer can quickly and directly measure the individual tree parameters that collectively describe the density and distribution of a stand's canopy foliage. Treating each tree crown as a simple geometric shape is possible, thus making canopies of complex, old-growth stands relatively easy to model in three dimensions.

Although treating crowns as solids may be inappropriate at fine scales, such simplification can provide a three-dimensional map of generalized tree crowns that collectively approximate stand-scale structure. For example, this level of structure modeling might help assess foraging conditions for an owl which flies between rather than through crowns. Although this model is a simplification of a complex canopy environment, it is a step toward the three-dimensional analysis necessary to understand the influence of canopy structure on arboreal processes and species diversity.

Measuring Canopy Structure: Crown Model Technique

Data for model development were collected in a Douglas-fir / western hemlock old-growth forest at the Wind River Experimental Forest in the southern Washington Cascade Range. The site is a relatively flat, moderately productive forest that originated 400-500 years ago (Franklin and DeBell

Figure 1a. Hemispherical photograph (fisheye photo) taken in a closed portion of an old-growth Douglas-fir/ western hemlock forest. The center of the image is directly above the camera, and the white circle represents 45 degrees below vertical. Note that significant light penetration occur at angles greater than 45 degrees.

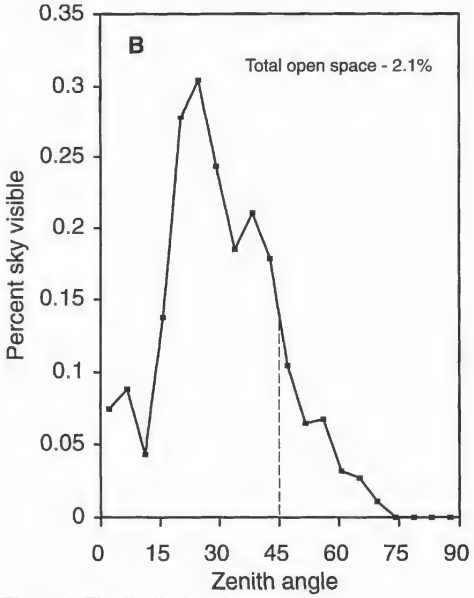


Figure 1b. The distribution of open space for the image in 1a. Maximum light penetration is at 25 degrees.

1988). The forest stand is near the upper limits of the western hemlock zone (Franklin and Dyrness 1973), with an understory tree layer dominated by Pacific silver fir (*Abies amabilis*), Pacific yew (*Taxus brevifolia*) and western hemlock. No detectable major disturbance has occurred since stand initiation, resulting in a multilayered forest. The largest trees are Douglas-firs up to 60 m tall and from 275-500 years old (Franklin and Waring 1980), and the western hemlocks occupy all strata from seedlings to old trees (Figure 2).

All trees taller than 50 cm were mapped for use in the spatially explicit model. This height was chosen because small seedlings can be ephemeral; population numbers do not stabilize until understory trees become well established (Van

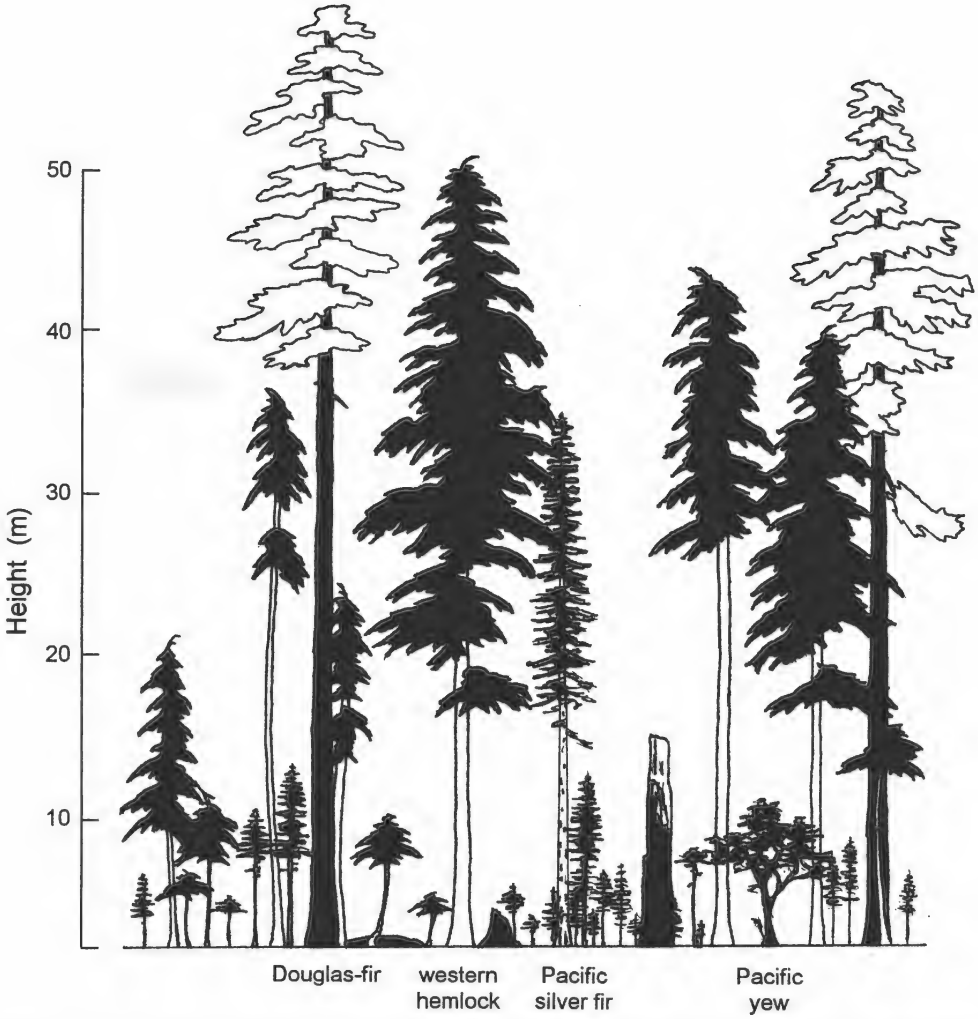


Figure 2. 50 x 20 m cross section of the study site at the Wind River Experimental Forest. Note the diversity of tree heights and the vertical distribution of the foliage.

Pelt, unpublished). Each crown was characterized by measuring the tree's height and height to the crown base, mapping the crown projection or measuring four crown radii, and assigning a crown shape (Figure 3). If a detailed view of the lower crown is required, height to crown base could be replaced by a value for the height to partial crown, the height to full crown, and the compass directions of the partial crown (North 1993).

Two 400 m transects were placed in interior portions of the forest. Trees greater than 5 cm in diameter at breast height (dbh) were mapped in a 20 m wide band centered on the transect line. Each of these trees was identified to species and also measured for total tree height, height to crown base, and crown radii. Trees taller than 50 cm were sampled in a 2 m wide transect centered on the same transect line. Although time permitted tree height measurements for only 85% of the trees, regressions of dbh by species on the 1429 measured trees were used to estimate the remainder (Table 1).

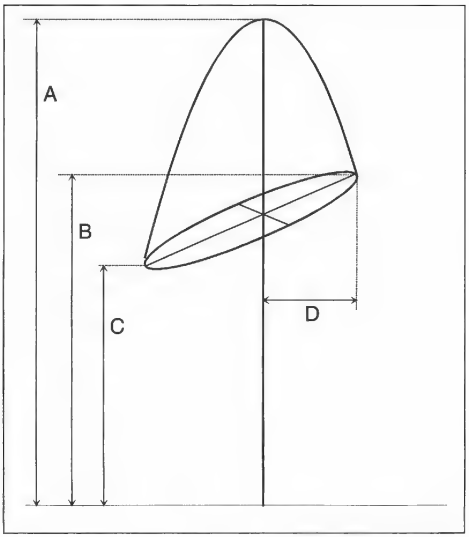


Figure 3. The variables required for the crown model: a, the tree height; b, height to full crown base; c, height to partial crown; d, four crown radii.

Data were also collected in a 0.2 ha circular gap in the Experimental Forest. This gap was cut as part of a larger study looking at the effects of experimental canopy removal on the forest understory (Van Pelt et al. 1992). All trees taller than 50 cm were mapped in a 0.4 ha area centered on the gap, and measurements for each tree followed the protocol used for the transect samples.

Crown Shape

For model construction, the crown of each sample tree was classed as one of several solid geometric shapes. No single shape can be applied to all trees because old-growth crowns are unique and irregular. Several simple forms, however, can be applied to most tree crowns.

Cones are perhaps the most commonly used shape for modeling conifers because they are easy to describe mathematically and are conformable to many crown shapes (Figure 4). In addition, most conifers and many broadleaf trees have conical shapes for the first several decades of their lives, and indeed many retain this shape for several hundred years (Horn 1971).

Cylinders are another group of geometric shapes that could be used to simulate certain tree crowns. Tall, closed canopy forest trees often develop deep, narrow crowns best represented by cylindrical shapes. Although young conifers are generally not flat topped, emergent old-growth trees can develop flat tops when they have stopped growing in height. The calculations for cylinders are simple and this shape should not be overlooked for appropriate situations.

Paraboloids are versatile shapes that are adaptable to a wide variety of crowns. These shapes can be used for trees that have either the deep crowns of main canopy trees, or the short, wide crowns of suppressed understory trees. In either case, the widest part of the crown is at or near the bottom of the crown, which makes paraboloids an appropriate choice.

Ellipsoids (including prolate and oblate spheroids) or truncated ellipsoids are similar to paraboloids in that they also approximate some old-growth tree crowns. A half-ellipsoid looks similar to a paraboloid of equal height and width, yet the paraboloid is narrower at all heights except for the bottom. Old-growth Douglas-firs often have ellipsoidal crowns, with the widest part of the crown low but not at the crown base.

Geometric shapes for each crown were selected in the field after viewing crown shape from several angles. All Douglas-fir tree crowns in this study were modeled as truncated ellipsoids, and all other trees are modeled as paraboloids. To

TABLE 1. Regression equations used to predict height from dbh for the trees used in the crown model; 1429 trees were used to develop the equations.

Species	Predicting equation	N	adj r^2
Tsuga heterophylla	$Ht = 50.863*(1-e^{-(.022*DBH)^{1.532}})$	693	0.947
Abies amabilis	$Ht = 45.59*(1-e^{-(.028*DBH)^{1.539}})$	468	0.958
Pseudotsuga menziesii	$Ht = 136.389*(1-e^{-(.003*DBH)^{0.6965}})$	149	0.746
Taxus brevifolia	$Ht = 17.542 / (1 + (5.367*e^{(-.086*DBH)}))$	119	0.604

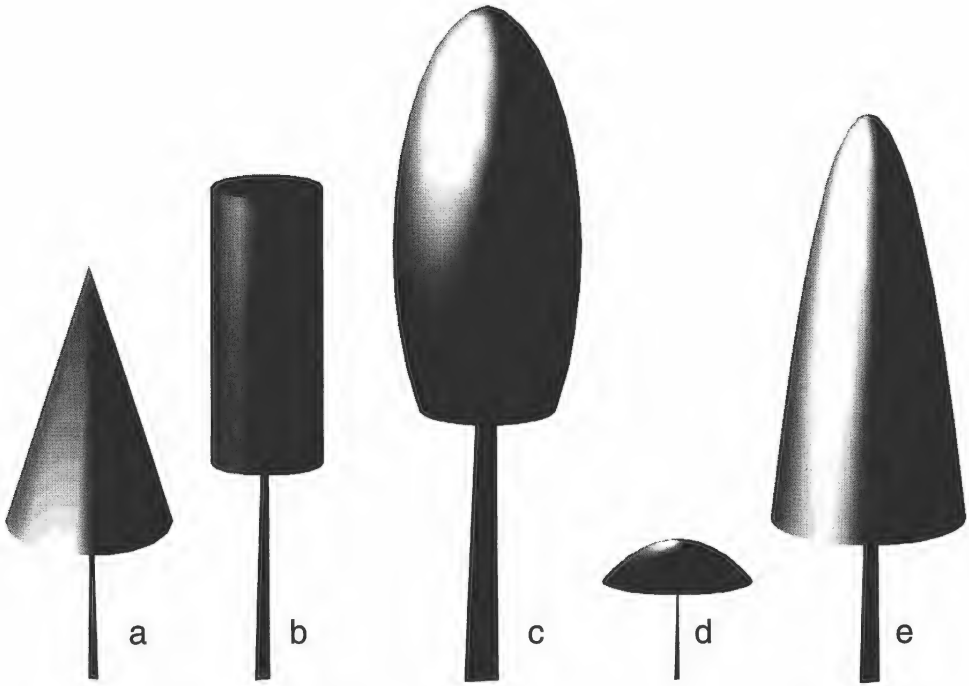


Figure 4. Potential crown shapes used in the model, from left to right: cone, cylinder, ellipsoid, paraboloid (wider than tall), and another paraboloid (taller than wide).

qualitatively assess the fit between actual crown shape and selected geometric shapes, photographs of 13 trees were digitally scanned. Two-dimensional silhouettes of the crowns were compared with the geometric shape selected in the field (Figure 5). The geometric shapes exclude irregular, lower branches and long branch tips, and fill in crown gaps where branches are missing.

The selected geometric shape, crown length, and crown radii were used to model the crown shape and height of each tree at its specific X-Y location along the transect. The resulting stand model closely approximates crown locations using specific height and position measurements, but it simplifies crown shape as a geometric solid.

Applications of the Crown Model

The following two examples illustrate how the model can be used to describe canopy conditions. The first estimates the vertical distribution of foliage based on measurements from the 20 x 400 m transects. This estimate is presented only to illustrate the model's capabilities because we do not have an exact measure of the real foliage distribution. The second example is a spatially explicit application that estimates understory light surrounding the experimental canopy gap. In this application, a subset of the model's results from specific locations are compared to fisheye photographs taken at the same locations.

Application I: Vertical Distribution of Foliage

The crowns for all trees along the transect were modeled and then horizontally sliced at 5 m height intervals. Crown cross-sectional area and volume were calculated for each tree at each interval. Frustum volumes were summed by species for each 5 m layer to estimate the vertical distribution of crown foliage. These data are presented in Figure 6 in two ways; graph A shows the total crown volume / ha at each height for each species;

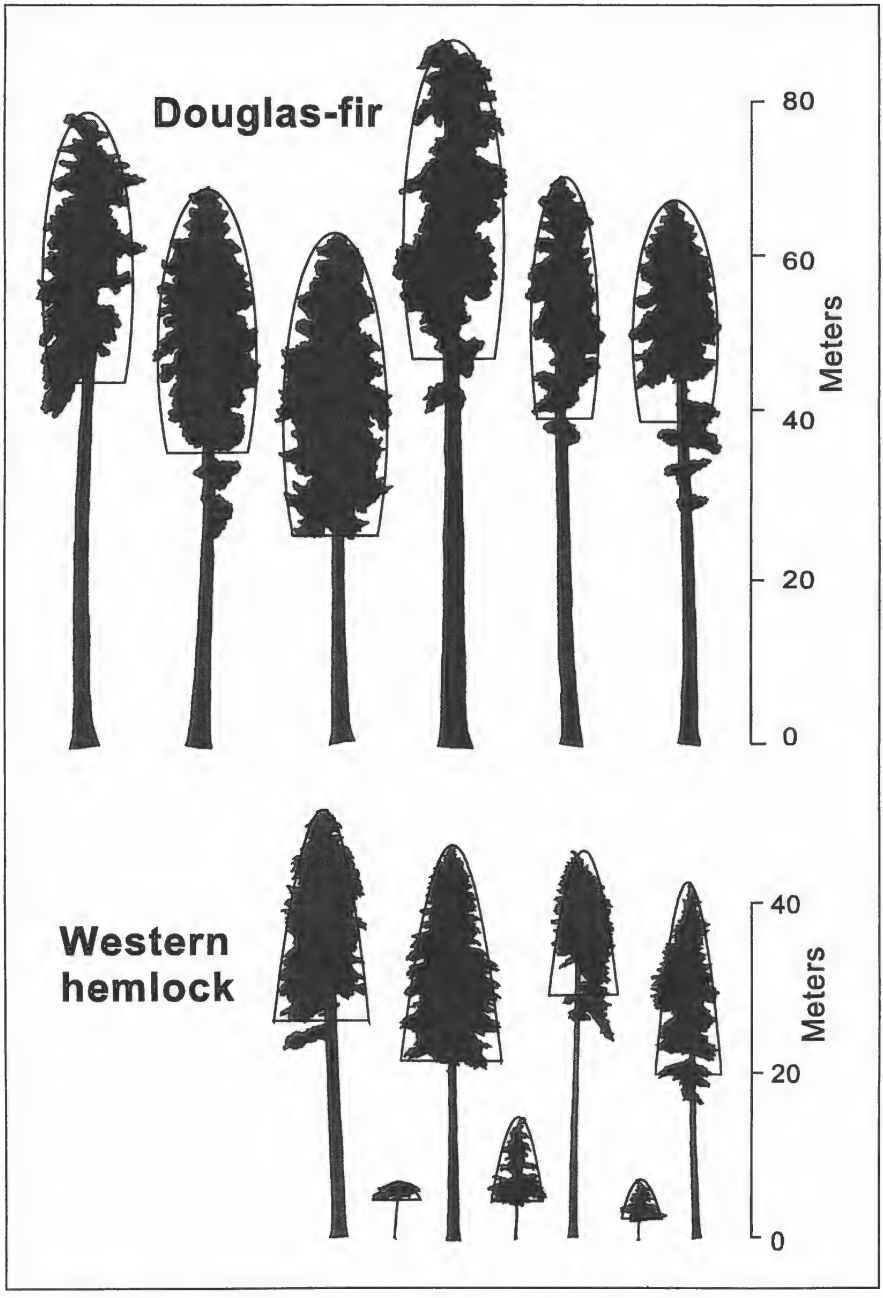


Figure 5. Top: Six photographic silhouettes of old-growth Douglas-fir trees with a truncated ellipsoid overlaid to show the model's approximation of the actual crown shape. Bottom: Seven photographic silhouettes of old-growth western hemlock trees with parabolic shapes overlaid to show the versatility of paraboloids for modeling a diversity of crown structures.

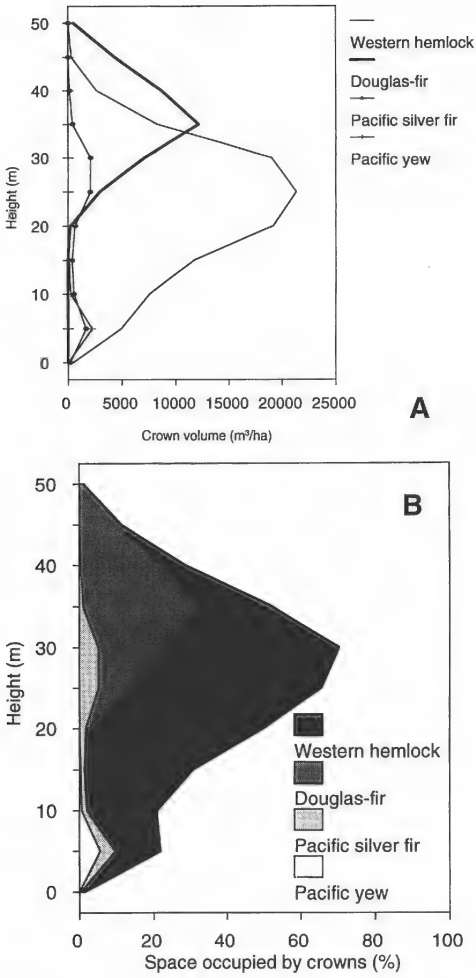


Figure 6. Vertical foliage distribution for the forest at Wind River: A, for each species individually in cubic meters per hectare; and, B, by species (individual shades), or total stand (outer boundary) as a percent of total available open space.

graph B is an area graph showing the total three-dimensional space occupied by each species by height interval.

The model helps visualize foliage distributions that cannot be measured with above-canopy remote imagery or understory light conditions. Slicing the canopy clearly showed that the highest density of foliage was between 20 and 42 m. Yet even in this vertical zone, 40% of the canopy space is open. Shade-intolerant Douglas-fir extends and dominates the upper canopy environment, providing most of the crown volume above 43 m. In total volume, however, the stand is dominated by western hemlock and in the lower canopy most of the space is occupied by hemlock crowns. In this stand, although large Douglas-fir may punctuate the outer canopy, most of the canopy structure is determined by the density and distribution of subdominant, shade-tolerant species.

Application II: Using the Crown Model to Estimate Light Reaching the Forest Floor

Hemispherical (fisheye) photography can be used to estimate the amount of light penetrating a canopy. Through the use of the crown model and a computer animation technique called ray tracing, a computerized equivalent of fisheye photos can be generated. From a selected point, the visible hemisphere's tree crowns are drawn by using the model, and the animation technique presents an overhead view from the ground. This view, similar to a fisheye photo, can be analyzed and the amount of visible open sky can be calculated. The ray tracing program (POV-RAY 2.0, 1993) models the light through the canopy by mathematically placing a camera, light source, and objects in three-dimensional space using ASCII text definitions. A window of a given resolution is defined and the program then calculates the path of light rays from each pixel back to the light source based on the reflective nature of the objects. Although ray tracing is commonly used for detailed photorealistic images, its accurate rendering of objects in three-dimensional space makes it useful for scientific illustration.

The canopy's effect on understory light was explored using the ray tracing techniques and crown models to simulate the canopy. To estimate light distribution throughout the 0.4 ha plot containing the experimental gap, ray-traced images were generated for 204 stations placed 4 m apart in each gap. A radial grid, like those used in fisheye photo analysis (Rich 1989), was imposed on each ray-traced image. By using the grid, the total percentage of open sky in each image was calculated. Each cell in the grid is analyzed for the percentage of the cell blocked by tree crowns, and cell percentages are summed over the image. The image for the gap center is shown in Figure 7A. This process is repeated for all images

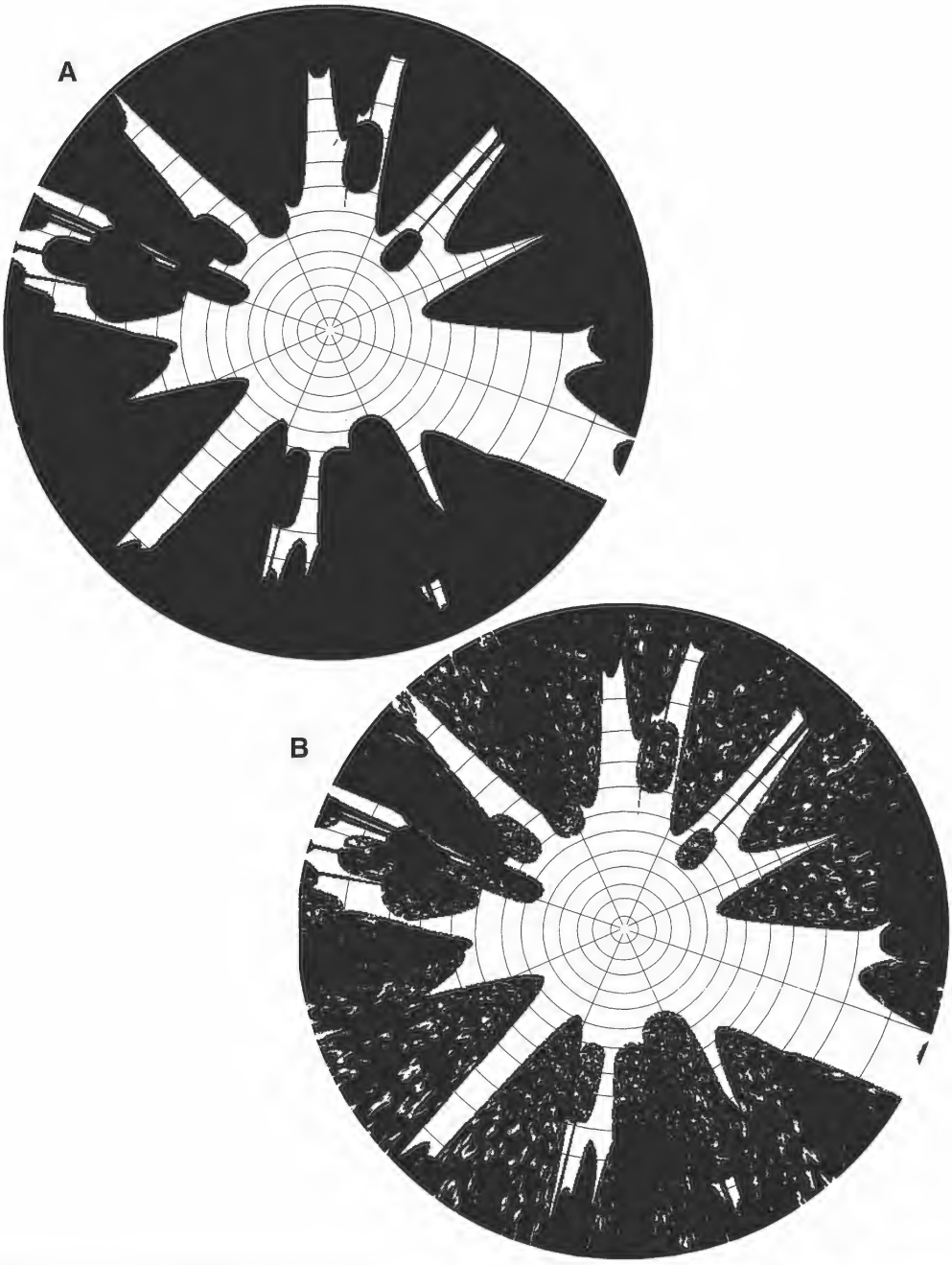


Figure 7. A, A simulated fisheye image taken from the center of a 0.2 ha opening in the Wind River old-growth forest (120 degree aperture); and B, the same image but with transparent textures added to more closely approximate actual conditions. Transparent textures were calibrated with a subset of actual hemispherical photos.

generated for each location and kriging is used to spatially interpolate the light distribution between the 204 stations.

A more accurate simulation of the light distribution can be made by using texturing techniques within the ray tracing program. Texturing lets the tree crowns transmit light in a more realistic manner. A subset of fisheye photographs taken from the Experimental Forest were used to calibrate tree transparency in the model. Figure 7B shows where this was done for the same location as Figure 7A.

To evaluate how well this application of the crown model simulates light transmission, comparisons of ray-traced images and fisheye photographs from the same location were made for 10 stations in two experimental gaps at Wind River. The fit between actual and predicted values of open sky were significant when summed either by zenith angles or by *azimuth* direction (Table 2).

TABLE 2. Regression statistics for comparisoins of actual fisheye photos with simulated fisheye photos. For the zenith angle regressions, N = 20; for *azimuth* direction, N = 8. All values are significant.

		Zenith angle		Azimuth direction	
Plot	Location	r^2	*p* value	r^2	*p* value
1	17 m N	0.988	<0.001	0.576	0.018
1	14 m N	0.992	<0.001	0.799	0.002
1	Center	0.997	0.001	0.789	0.004
1	14 m S	0.473	0.001	0.897	<0.001
1	28 m S	0.962	<0.001	0.928	<0.001
2	25 m N	0.999	<0.001	0.786	0.002
2	13 M N	0.998	<0.001	0.966	<0.001
2	Center	0.989	<0.001	0.972	<0.001
2	13 m S	0.919	<0.001	0.817	0.001
2	25 m S	0.982	<0.001	0.851	0.001

Once the entire array of locations has an image, surface maps of the distribution of open sky by percentage throughout the gap were generated using a geographic information system (ARC/INFO, v. 6.1.2, 1993). This can be combined with a model of the amount of diffuse radiation distributed across the sky to estimate the total amount of diffuse radiation that is penetrating the canopy. The ratio of this to the total amount of diffuse radiation in an unobscured sky is known as Indirect Site Factor (ISF). The ISF is a measure of diffuse light conditions in the understory, which in our example occurs at the center of the opening (Figure 8A).

To investigate the influence of latitude on understory light distribution, sun-paths throughout the growing season were modeled. This measure provides an idealized value (i.e. no cloud cover) of direct light conditions in the gap (Figure 8b). The maximum direct light possible over the entire year (Direct Site Factor, DSF) is 0.325 and is shifted 17 m north of the gap center. The 0.325 value means that 32.5 percent of the possible direct light reaches that spot, given no clouds or haze. The shift indicates that light filtering through tall Pacific Northwest forests influences understory conditions at an oblique angle to the forest floor. Simple vertical or horizontal measures will not give an accurate assessment of tree reponse to canopy gaps, because the changes may be completely shifted out of the gap. This result is similar to that presented by Canham et al. (1990), who modeled gaps as cylinders at the same latitude.

Discussion

The measure of an ecological model is its ability to accurately illuminate complex processes at the expense of some simplification. Powerful computers and new statistical techniques have made three-dimensional modeling of the forest canopy possible. Yet these models will always be built on some simplified measurments of canopy structure determined by the selection of scale and access method.

Because the model is a simplification of a complex structure, the model is meant for stand-scale research, not for detailed analyses. Crown shapes are treated as solids in this model, yet foliage density within a single crown is actually distributed as a foliage shell of variable thickness (Jensen and Long 1982). For young trees and shade-tolerant old trees, the inside of the shell is an area of high shade and is thus largely photosynthetically inactive. Old trees, however, have unique branching patterns and can develop very open crowns. At the stand scale this variability is minimized, but more detailed models will be needed if a closer examination of forest structure is required. For old-growth tree crowns, attaining the next higher level of detail is a major step that will require modeling tree crowns through their individual branches. Such a model would require numerous

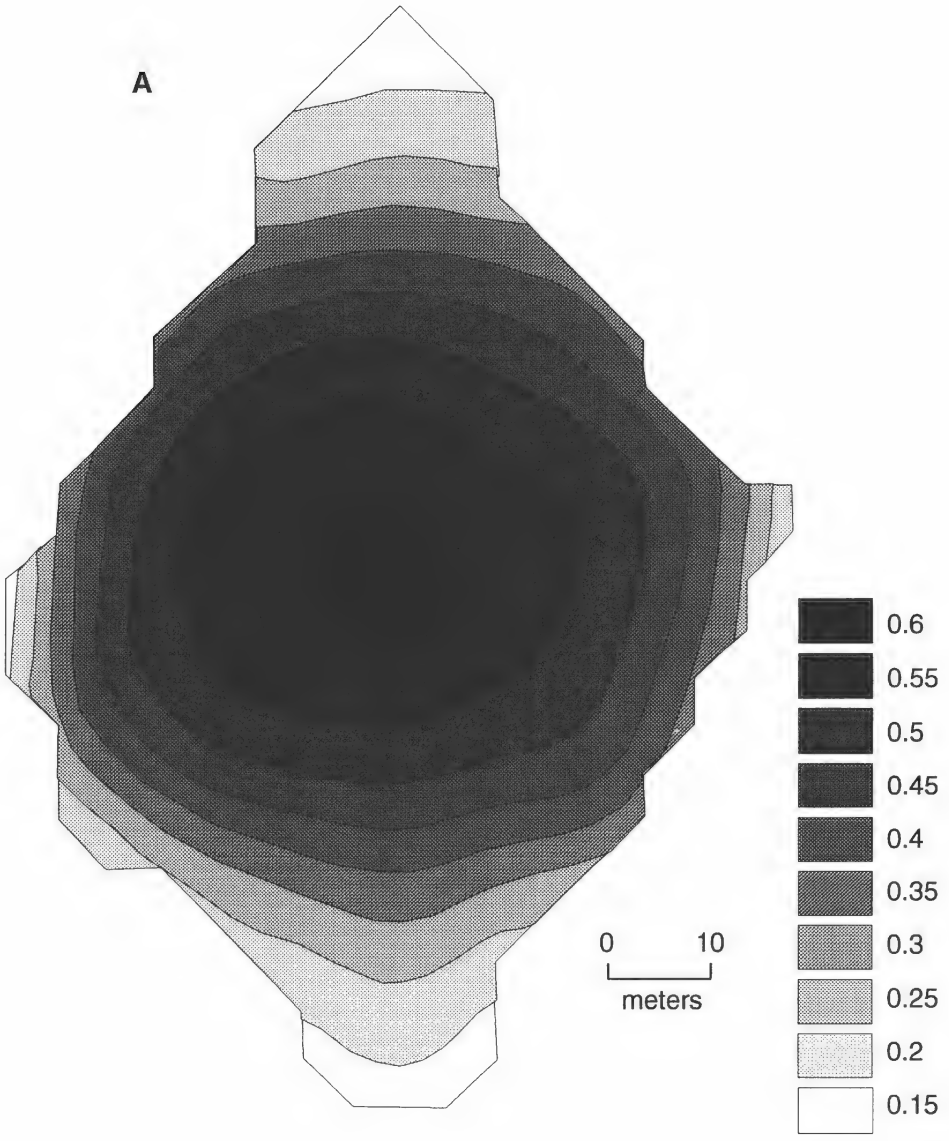
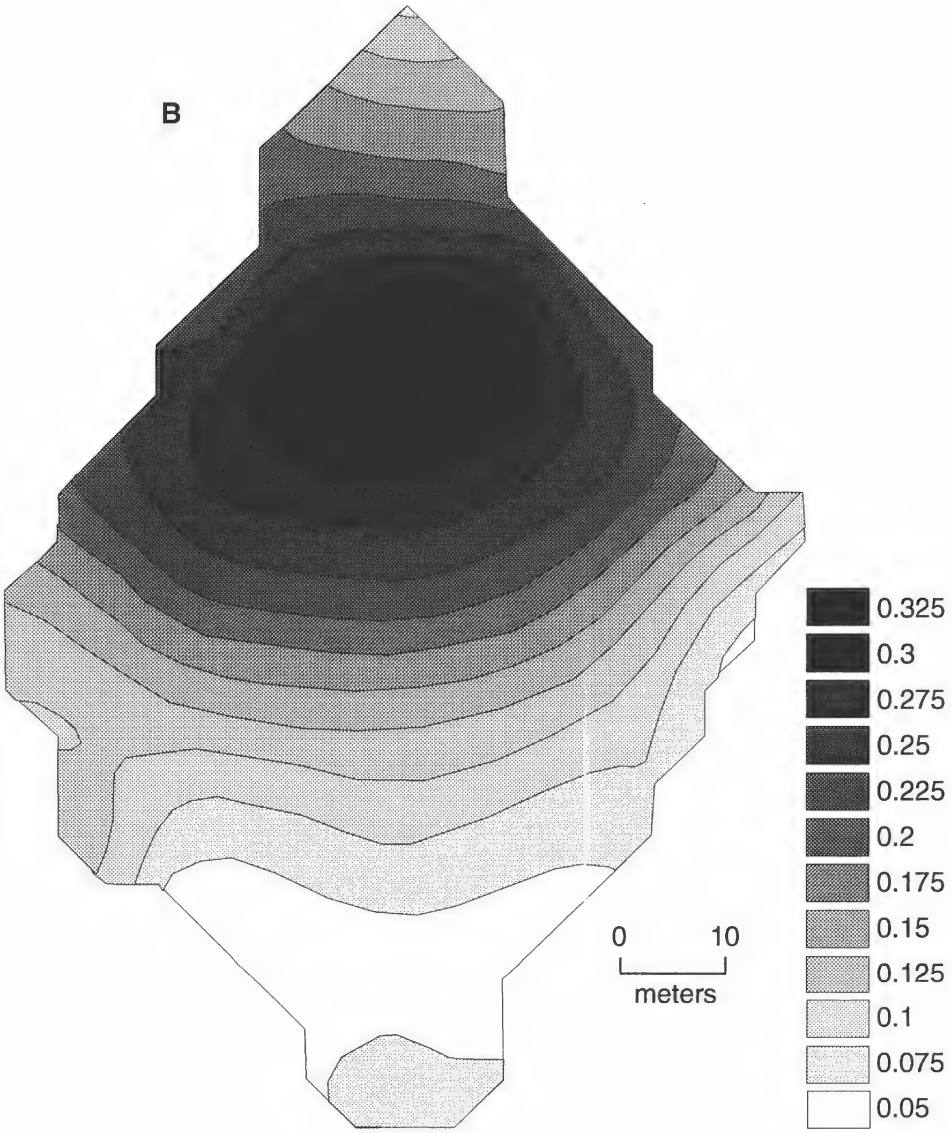


Figure 8. A, Results of the diffuse light model. Indirect Site Factor for a 0.4 ha area surrounding the 0.2 ha gap. The outer boundary is the limit of the plot and the irregular white line represents the crown projections of the remaining canopy trees. The gap center has the highest ISF. B, A direct light model showing the percentage of possible direct sun (Direct Site Factor, DSF) over the course of a growing season. This analysis makes no predictions for clouds or haze. The maximum value is shifted 17 m north of gap center.


B
0
10
meters
0.325
0.3
0.275
0.25
0.225
0.2
0.175
0.15
0.125
0.1
0.075
0.05

measurements within individual crowns, rather than a few easily measured crown dimensions.

The applications presented describe two of the many potential uses of this model to stand-scale research. Two applications illustrate how crown volumes are vertically distributed and how crowns affect light penetration. The next logical step for this application is to combine the vertical distribution with horizontal spacing of trees to come up with a three-dimensional analysis of crown distribution. A corollary to this approach is an analysis in three dimensions of the open space within the forest canopy. For arboreal species such as the northern flying squirrel (*Glaucomys sabrinus*) or the northern spotted owl (*Strix occidentalis caurina*), the amount and distribution of open space may be important to movement or foraging success (Carey 1985, Rosenberg and Anthony 1992).

The computer-generated hemispherical photos also have wide applicability. Not only can large areas be analyzed once the stand parameters have been mapped, but analysis of canopy openness at various vertical locations is easily accomplished, an aspect that has limited canopy photography from the ground. Simulations of proposed harvesting activities is yet another application of the light model. Selective logging, green-tree retention, strip cutting, and other forestry practices can be simulated under current and future conditions.

At present the accuracy of the model is difficult to assess because there is no absolute measure of canopy structure. Unlike ground-level forest structure, the canopy environment does not readily imply a standard unit of measure. A stand's basal area is easily sampled because tree boles are discrete structures. Tree crowns, however, can be considered a fractal shape (Zeide 1993) because their dimensions will change depending on the size of the sample unit. Any model's representation of the canopy is relative to the scale it works at and the size of its smallest sample unit. The crown model presented is for stand-scale assessment of canopy structure using individual tree crowns which are treated as simple geometric solids. Given these parameters we believe the model can help visualize patterns in canopy structure which could further a more analytical exploration of the canopy environment.

Conclusion

Studies of forest structure have often focused on tree stems, and the function and composition of the immediate environment near the ground. In a plant community where the vegetation is 30 to 80 m tall, however, many of the dynamic ecological processes and biodiversity will occur in the arboreal environment about which little is known. Before the ecological interactions of species and processes can be linked with their environment, a measure of the aggregate crown or stand-scale structure is needed. This measure would have at least three benefits: until most of the species and complex interactions of an ecosystem are well studied, measures of structure must often serve as a surrogate measure of function or biotic diversity; for experimental design and sampling, researchers need to know how the canopies of different stands are distinct and what factors make them so; and most monitoring, planning, and management of forests are at the stand scale. A measure of canopy structure that uses ground-based methods would provide foresters with a means of comparing canopy environments between different stands.

In this paper, we present a method for modeling old-growth forest canopies at the stand scale using ground-based measures. This technique is based on easily measured crown dimensions and can aid in three-dimensional analysis of forest processes. Two applications of the model were used to examine the vertical distribution of foliage and understory light levels in a Pacific Northwest old-growth forest. The model indicates that much of the foliage mass in the old-growth sample stands is dominated by shade-tolerant, subcanopy species, and that light conditions for a point on the forest floor are more influenced by the canopy's structure at an oblique angle than the tree crowns directly overhead. We believe the model can help researchers analyze the complex structure of the overstory environment as they explore the ecology of the canopy frontier.

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Silvicultural Systems Design with Emphasis on the Forest Canopy

Abstract

Silvicultural manipulation of an individual tree canopy, or the live crown, controls the quality and quantity of growth. The growth of trees can be controlled by these manipulations only if clear objectives are defined as measurable parameters. The principles of crown management (e.g., juvenile spacing, commercial thinning, pruning) are well known but have only recently been expanded to include wildlife and other non-timber objectives. Silviculture impacts ecosystem functions of the forest, particularly in the forest canopy. As forest resource management is constantly revised to meet broader range of goals (e.g. habitat maintenance or restoration, watershed functions, carbon sequestration) a systems approach to these operations becomes necessary. A silvicultural system approach is summarized by system design, performance, and tolerance of measurable criteria. Monitoring determines if elements of the system are in predetermined bounds, or control. This active management brings the forest canopy in line with target objectives at numerous temporal and spatial scales. There are many scales (temporal and spatial) and methods of control. Common silvicultural manipulations are used to demonstrate canopy control for wildlife habitat maintenance and restoration at the individual tree level. Landscape level distribution of habitat structure and composition is achieved by retention of various amounts and patterns of forest. Updating and adapting management to either better meet stated goals or modify expectations is a continuous process. Forest management, in this context, becomes a powerful research tool that provides useful results in a timely manner.

Introduction

This paper discusses some of the common uses of canopy manipulation to achieve wood quality, briefly describes historical canopy control in the forest industry and, extends the concepts of silvicultural systems to the control of wildlife habitat functions. The purpose of the paper is to offer a new perspective on the application of silviculture. Silviculture can be quite active and provide very specific objectives but clear, measurable design criteria (e.g., height above ground, density of snags (number per hectare), or size of cavity opening) are required.

Silvicultural manipulation of an individual tree canopy, or the live crown, controls the quality and quantity of wood produced. The principles of crown management, such as juvenile spacing, commercial thinning, and pruning have been applied for timber objectives (Petruncio 1994, Oliver et al. 1986). Only recently have canopy manipulations been viewed from the wildlife or landscape perspective. Many conventional silvicultural measures are characterizations of the canopy, such as live crown ratio (LCR), crown closure, and canopy cover. Commercial thinning typically coincides with crown closure to ensure consistent radial growth of logs. Pruning up to 60 percent of the live crown while the stand is still young maximizes the production of high value clear wood in logs (Smith and Long 1989, Briggs and Fight 1991, Petruncio 1994) but is also keyed to canopy closure and total tree height. Proper timing of silvicultural manipulation delays or prevents stagnation of the forest, which minimizes reductions in growth (and development) and perhaps improves fire resilience of the residual stand (Agee 1993).

Simple height-age charts or estimates of the site index establish the baseline against which actual stand values can be compared. These charts may be improved if they were calibrated by canopy measurements including LCR and percent cover as indicators of forest health and vitality.

Silvicultural decisions are more typically keyed to diameter outside bark at breast height (DBH) because it is fast and easy to measure. A more sensitive measure of growth uses 5-year radial increment: Successive declines in the previous 5-year radial increment indicate, among other things, that crown competition—canopy crowding—is affecting growth and signals an appropriate time for thinning operations. Thinning the canopy density provides two unique benefits: (1) even diameter growth (less variation in annual ring width) for improved wood quality and (2) more efficient use of the live crown by reducing competing trees of inferior quality and lower vigor. But there are numerous other functions harboured in the structure of the crown.

Canopy structure of the forest community holds the key to maintaining populations of a number of plant and animal species. These structures include snags, cavities, thick bark, loose bark, tall stems, branches, leaves and twigs, dense foliage, layered canopy and downed wood (Balda 1975, Mannan et al. 1980, Lundquist and Mariani 1991). Habitat structures of trees could be used in a system of diagnostic criteria regarding their function (Table 1). Birds and mammals use the different structures in the forest for food, nesting, and denning requirements.

Many Pacific Northwest forest ecosystems have been so severely simplified by intensive management that an active approach of restoration may counter declining plant and animal populations. Currently, forest practices in the Pacific Northwest are moving forward with unproved methods. The call for ecosystem management is based on observed declines in habitats and species, and threats to air and water quality. Structural diversity in managed forest canopies will be improved with various levels of retained green trees and snags, as well as varied spatial aggregation of the leave trees. Conventional thinning techniques combined with new innovations in creating canopy structure can be used to improve wildlife habitat.

Silvicultural manipulation produces large dimension trees that can serve as nest trees. In managing for cavity and bark nesting birds, characteristics of foraging habitat should not be overlooked. Canopy structure is often the primary determinant of habitat preferences by wildlife. Snag density is important with regards to wildlife utilization (Bull et al. 1980, Bull et al. 1990). Woodpecker populations can be managed through provision of various snag densities (Balda 1975, Bull and Meslow 1977, Thomas et al. 1979, Nietro et al. 1985).

Design of Silvicultural Systems

Managed stands can be viewed as single replicate experiments or demonstrations if the objectives for stand development are stated as hypotheses. The many harvest units that include retention of live and dead tress in the region are operational experiments but few planners have had the foresight to make reasoned projections about the effects of retention on canopy dynamics, let alone

TABLE 1. Habitat structures of trees and their function

Structure	Function	Source
Broken top snags	Nesting platform for osprey and eagle Expedites snag softening for cavity excavation	Miller and Miller, 1980
Large diameter snags	Forage for woodpeckers Nesting and roosting for woodpeckers and owls	Thomas et al. 1979, Bull 1978
Large diameter live trees with thick bark	Abundant arthropod fauna (forage for brown creeper and nuthatches)	Mariani 1987
Large diameter live trees with thick branches	Nest sites for marbled murrelet and arboreal rodents	Ritchie 1988
Multi-layered understory (space between layers)	Habitat for aerial insectivores such as Vaux's swift	
Loose bark	Bat roosts Brown creeper nests	Christie and West 1993 Mariani 1987
Cavities	Nest sites for secondary cavity nesters	Bull 1978
Mistletoe brooms	Nest sites for arboreal rodents and murrelets	
Heartrot-infected bole of tree	Woodpecker drumming and nest excavation	Bull 1980
Diversity of vegetation heights (also called layers)	Diversity of arthropods and insects	
Flattened, fan-shaped branch arrays	Provides horizontal surface for development of epiphyte communities. The western flycatcher, brown creeper, hermit warbler, and kinglet all use epiphtyes for nest construction.	

measure the key variables. Focus has been on tactical operations and less on long-range strategic implications. Hypothesis generation should begin by recognizing that harvest units are experiments in the control of canopy and ecosystem processes.

Silvicultural systems have several elements; system design, design of performance parameters or design criteria, and design of tolerance levels important to assure the control of the overall goals (Taguchi et al. 1989). System design avoids loss from unexpected deviation from target values. Parameter design develops measurable criteria to answer operational questions. Tolerance bounds are necessary to assess the system.

System design determines the life cycle, or time frame, and processes involved; typically, a timber harvest rotation in forestry. The system may maintain a constant supply of snags of a variety of sizes and species. Other ephemeral structures in the canopy include cavities that disintegrate because of decay but are critically important to wildlife (Bull et al. 1980, Ruggerio et al. 1991). *Parameter design* details levels of controllable measures with which to monitor system performance. Silvicultural variables are, for example, height or diameter growth, canopy cover, and survival of residual trees and seedlings. It is important to include ecological variables such as the number and use of natural and manufactured nests, level of epiphyte production, and habitat use by canopy strata. *Tolerance design* specifies the level of variability for parameters; narrow tolerances assure close adherence to system targets but often at much greater financial cost. The results of monitoring are used in the continuous revision and improvement of the system design (Depta 1984, Dyson 1990). A more advanced notion accepts only increasingly narrow tolerances, if at all, so that systems are continuously improved.

The long range nature of forestry makes some of these decisions difficult. On-line experiments (Taguchi et al. 1989) are done in the course of growing the forest and can be used to assess, in a timely manner, the practicality of ecosystem based forest management. Off-line research, by contrast, stops production while experiments are completed. The contemporary methods being practiced to recover at least some of the complex structure and function the forest canopy involve some fashion of tree retention based on the management hypothesis that much of the function of forest structure is in the canopy. Silviculture needs the application of sound, tested methods. Mixed species and structurally complex stands (Raghavan 1993, Rose 1993, Wampler 1993) are examples where the benefits of on-line canopy experimentation can be applied—while the stand is developing measures can be made to address specific hypotheses. Wood quality and growth are well understood for most tree species in the Northwest; canopy manipulations need to test conjecture about the value and use of manufactured habitat structures (as per Table 1). The next step in silviculture develops a common framework for monitoring, adjusting methods, and communicating results across all of the players involved; agencies, companies, first nations, and citizen groups (Walters 1986).

Scales of control of the forest canopy range from the landscape down to the stand and to the individual tree. We may measure the percent cover of vegetation (e.g., by species, age, land use) and describe basin scale structure in terms of the distribution of the patch type and size; the canopy as sensed from above (Ciesla 1989, Greer et al. 1990). With the larger spatial frame often a longer temporal frame is also needed to see the influences of canopy manipulations (Spies and Cohen 1992, Hudson 1988). Canopy resolution from digital remote imagery is coarse and still requires ground based validation. As the resolution is reduced at the larger scale, measures such as percent canopy cover and sustainable flow of wood are important. The latter requires that harvest settings are designed efficiently and properly placed within the landscape to control landscape level targets of canopy composition and structure.

The ground work of ecosystem management is at the stand level (typically 20-100 ha.) because it is at this level we can control the canopy functions and the growth of trees. There are two distinct spatial patterns of canopy retention (also structural retention, STR, after Berg and Schiess 1994): dispersed trees, widely scattered throughout; and aggregated trees (also called clumps, patches), that may be connected to the uncut forest. Each pattern can be evaluated at different levels measured by residual density (trees per hectare, basal area per hectare), percent canopy cover, or residual percent of stand volume. Functions differ with spatial pattern; dispersed canopy moves

toward a multilayer stand over time while the aggregated canopy offers immediate refuge and islands of less disturbed forest conditions. Prescriptions (management direction based on sound, reasoned diagnosis) may be linked at larger spatial scales but the essential building block will be the stand treatments.

Within each individual tree canopy there are also structures that can be measured only at that scale. Because of the thermal and moisture gradient through the length of a canopy, there is a variety of niche spaces. The canopy birds need perches, hiding cover, and cavities that develop from specific microclimatic conditions and vary by the tree species, age, spacing, among other variables. It is important to be clear about the specific location that one expects to see differences resulting from of canopy manipulation.

Methods of Control integrate forest resource management with research methods. Empirical studies of forests are difficult to design and are expensive to implement with often limited application to the broad range of conditions in the region. Working knowledge of how to implement innovations in forestry is accelerated by providing operational examples—on-line experiments (see page 7).

Wampler (1993) and Rose (1993) concur with Isaac (1943) and suggest that STR impairs height growth of Douglas-fir and alters species composition; light is the limiting factor for growth. Issac (1943) states that 50 percent canopy cover (ca 50 trees per hectare, TPH) reduces mean annual height of Douglas-fir growth by 50% compared to the clearcut conditions. Secondary influences (e.g., below ground competition, crown architecture, MAI, % volume growth) are often only discussed (after Long and Roberts 1992, Birch and Johnson 1992) but are poorly understood. Projection of how a retention silvicultural system is expected to perform might use height growth equations and site index curves (e.g., King 1966) to predict the development of the new forest. The response of overstory trees released from competition might be measured by diameter increment. Wood quality of both individual trees and the whole stand might be hypothesized to improve because of the release of growing space in the canopy.

Mortality of the trees retained at harvest can be expected but risk of windthrow might be reduced by leaving trees with low height to diameter ratio, Ht./DBH, usually the dominant and codominant crown classes (Franklin 1963). The live crown ratio (LCR=crown length/total tree height) may be another indication of the wind resistance of a tree and could be used to make decisions about retention. The pattern of leave-trees can follow common rules for placement on the landscape to minimize weather effects.

Monitoring canopy modifications is important in managed forests with elevated levels of structural diversity. But these activities are time consuming and costly (Shaw et al. 1993) emphasizing the importance of describing the exact measurements. Efficient monitoring uses all of the information collected and is an adaptive process that may need refinements over time.

Conclusions

Foresters must constantly revise their methods (Walters 1986); updating and adapting management to either better meet stated goals or modify expectations. Forest management in this context becomes a powerful research tool that provides functional results in a timely manner (Depta 1984, FEMAT 1993). A look to the past indicates that the nature of timber management has changed and the harvest operations are now far more constrained by concern for ecological function. The large dimension, high value old-growth timber is rare and reserves for bird and fish protection are scant. The forward looking forest manager may define a future condition where silviculture and harvesting technology are viewed as critical elements in canopy operations designed for endangered species protection and recovery (Mitsch and Jorgensen 1989).

We can determine the wildlife species that will benefit by planning for structural retention, buffering harvest areas, and canopy modification, however, the use of canopy structures by wildlife is still being described for many animals. If the research can be merged with operations, our collective wisdom about proper harvest and management improve at a rapid rate.

This strategic view is reflected in the contemporary use of large area plans to properly place roads and harvest settings in the landscape. The challenge for the future will be to adapt existing technology and develop new tools that meet increasing constraints of regulations and land ethic.

A critical point is that methods and structures be described in a common language between the roles (managers, loggers, engineers, foresters, ecologists). Honest and open dialog about the success and failures of innovative practices, not litigation, will communicate the goals and perhaps improve our ability to live and work in the forest. As the functions of the forest canopy become more evident this communication will be increasingly important as people from many disciplines work together.

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Canopy Microfungi: Function and Diversity

Abstract

Microfungi are an inconspicuous but important component of the biota of forest canopies. Within canopies, microfungi are found inhabiting living and dead foliage, bark, and wood, and are also associated with canopy epiphytes and arthropods. As epiphytes on foliage and twigs, microfungi serve to concentrate dilute organic nutrients. Biomass and annual production by epiphytic microfungi can approach 500 kg/ha and may represent a significant food resource for microarthropods. Saprotrophic decomposers contribute to in situ decomposition of perched litter. Fungal endophytes occupy healthy, asymptomatic foliage and stems. Some of these fungi also produce compounds antagonistic to insect herbivores. Canopy microfungi may also provide a minor link between soil and aquatic food webs as early colonists of live foliage and twigs that complete their sporulation cycles in soil or streams and as a portion of annual aboveground production that is assimiliated in soil as litterfall. The varied components and functions of canopies with which microfungi are associated suggest that biodiversity of the microfungal biota is high and potentially a rich source of novel taxa.

Introduction

The canopies of mature, old growth forest trees present a complex, multilayered habitat that supports a rich and varied community of organisms. Microfungi are an integral component of this community, interacting in a variety of ways with the host tree as well as the other organisms that together comprise the canopy community. For two of the authors (JKS, MAS), investigating the fascinating, complex roles of fungi in the forest canopy provided an early introduction and apprenticeship in mycology that became a lifetime career interest. Microfungi in canopies are more than objects of biological curiosity, however; they play important ecological roles in mature forests: nutrient cycling, symbioses with canopy epiphytes, and symbioses and trophic interactions with arthropods and other canopy microfauna.

Much fundamental information on the roles of fungi in canopies remains fragmentary, a problem that presents many opportunities for new and significant discoveries. Microfungi in canopies form a variety of direct associations with the host trees, colonizing foliar and twig surfaces (epiphytes), internal foliage (foliar endophytes), young and old bark (bark endophytes) and wood (xylem endophytes and wood decomposers). The distribution and diversity of microfungi in forest canopies is also influenced by epiphytic cryptogams, phanerogams, and arthropods and other canopy animals, which also interact in a variety of associations with canopy microfungi. Decomposition and nutrient cycling processes (such as in situ epiphyte decomposition, dead limbs, lodged needles, perched soil) occur within canopies, but little information has been published on these processes and the roles of microfungi in them. Although many species are uniquely adapted to biotic functions and conditions specific to the canopy habitat, the total canopy mycobiota also includes species with widespread terrestrial distribution. More intensive investigations will undoubtedly reveal a multitude of specialized, highly adapted endemic microfungi, and inevitably many new taxa.

Diversity of microfungi occurs at an exceedingly small scale—a single conifer needle may harbor several dozen different species externally and internally. Although microfungi are ubiquitous in nature, they typically are inconspicuous: usually they are present as internal, unseen, microscopic hyphae and their presence is revealed externally only when they sporulate, usually seasonally and typically ephemeral. Many are highly host- or substrate-specific. Conventional sampling methods of vegetation ecology are inadequate to

accurately enumerate microfungi, and the details of distributions of even the more familiar taxa remain sketchy. Laborious isolation procedures are generally required to detect and quantify them. Identification requires microscopic examination, and generally requires a high degree of expertise. Often identification is difficult or impossible with isolates in pure culture that fail to produce spores or identifiable structures. Conversely, certain groups do not grow or sporulate in culture (e.g., Metacapnodiales), and must be detected visually on host substrates. A particular obstacle to ecological studies of canopy fungi is that often basic taxonomic information is lacking or insufficient. This problem can only partially be overcome by integrating existing databases—fundamental biological survey work is also needed. Differentiation of individuals of a fungus species adds yet another level of complexity. Because of the ability of fungal hyphae to anastamose and become multinucleate, and the ability of many fungi to reproduce asexually, enumeration of individuals often can only be accomplished using specialized techniques of molecular genetics.

Foliar and Twig Epiphytes

Communities of epiphytic fungi in canopies develop as a result of the same types of biotic and abiotic interactions at play on non-arboreal substrates, with the exception that new uncolonized substrates are predictably and regularly added by new seasonal growth. Foliar and bark surfaces provide substrates that support characteristic assemblages of specialized microepiphytes that undergo changes in species composition and biomass as the substrates age. Particularly in more mesic habitats, microepiphyte assemblages can become well developed, especially on evergreen foliage and twigs, where they may attain a substantial biomass and annual productivity. Carroll (1979) estimated biomass of fungal foliar epiphytes in an old-growth Douglas-fir forest at 30 kg/ha, and Carroll et al. (1980) estimated fungal twig microepiphyte biomass at 12-20 kg/ha. Annual production of fungi on combined twigs and needle surfaces was estimated to be 450 kg/ha. (Carroll et al. 1980).

Although mesic, foliar surfaces experience extremes of temperature and desiccation seasonally and diurnally. Epiphytic fungi are adapted to xeric conditions and low levels of nutrients that are either leached from foliage or intercepted in rainfall. Most fungi in exposed habitats have melanized hyphal walls, grow sporadically in response to temporally favorable conditions, and are specialized to withstand exposure and desiccation. Needle surfaces typically are colonized by familiar, ubquitous epiphytes common on many plants: such genera as *Epicoccum*, *Alternaria*, and *Hormonema*. *Atichia millardetii* Racib., the anamorph of *Seuratia millardetii* (Racib.) Meeker, a loculoascomycete that grows as a yeast-like mass in a gelatinous matrix, is a dominant epiphytic species on twigs and needles of several conifers in the Pacific Northwest (Carroll et al. 1980). On some hosts, sooty molds (*Capnodium*, *Metacapnodium*) occur in association with scale insects and are nourished by exuded honeydew (Hughes 1976).

On conifers, such as Douglas-fir (*Pseudotsuga menziesii* (Mirb.)Franco), the topology of needle surfaces influences distribution of microepiphytes, with greater colonization near the needle midrib, near stomata, and along the margins of anticlinal cell walls (Bernstein and Carroll 1977; Carroll 1979). Microbial biomass tends to increase with needle age through the first three years. In this exposed habitat, these fungi are also available as a food resource to grazing microarthropods, such as orabatid mites, and grazing may help explain the decreases in microbial biomass observed on older needles. Distribution of microepiphytes also tends to decrease with increasing height in the canopy (Carroll 1979). Microbial biomass on twigs similarly increases with age (Carroll et al. 1980).

Specialized Parasites and Pathogens

Common microfungal parasites and pathogens of foliage and twigs of northwestern conifers are described in detail in Funk (1981, 1985). A recent host index (Farr et al. 1989) lists approximately 80 species of microascomycetes, 50 species of hyphomycetes, and 30 species of coelomycetes associated with the foliage and twigs of Douglas-fir alone in the Pacific Northwest. This list should be considered partial because routine isolations from Douglas-fir and other conifer hosts often yield taxa not listed (Stone, unpublished). Endemic pathogens are not uncommon in the foliage of mature trees, but they often have disjunct distributions, apparently affected by site factors and individual host genetic susceptibility.

Phaeocryptopus gaeumannii (T. Rohde)Petr. and *Rhizosphaera kalkoffii* Bubák, for example, are commonly found infecting a proportion of the needles of mature Douglas-fir trees, but their effects are not often serious unless other sources of stress, such as drought or cold injury, are involved. In young plantations and non site-adapted genotypes, however, these fungi can cause serious defoliation.

Another group of foliar fungi are primarily superficial but also invade the inner spaces of foliage. Such colonization may be confined to stomatal chambers or may involve extensive intercellular hyphae in mesophyll parenchyma. Microthyriales or "fly speck" fungi have flattened, shield-like ascomata produced on living needles. Black mildews, such as *Meliola*, *Asteridiella*, and *Rasutoria*, are typically superficial, but sometimes produce hyphae that enter needles at the stomata or pierce epidermal cells. Again, presumably because of the exposed habitat, the hyphae of these fungi are melanized. *Phaeocryptopus gaeumannii* commonly infects needles of Douglas-fir and produces extensive superficial and internal hyphae (Stone and Carroll 1986).

Foliar Endophytes

Fungal colonization of internal tissue of apparently healthy foliage, particularly of plants with evergreen or long-lived foliage, has been well documented. Such endophytes are a ubiquitous, ecologically specialized group of symbiotic fungi and are widely assumed to be present in virtually all land plants (Carroll 1988). Inhibition of herbivory by toxic alkaloids produced by endophytes infecting certain grasses has been demonstrated (reviewed by Clay 1988), and forms the basis of a mutualistic symbiosis in these hosts. Several fungus species isolated as endophytes from coniferous foliage and bark also have been shown to produce biologically active compounds (Bills et al. 1992; Polishook et al. 1993; Stierle et al. 1993), including compounds toxic to defoliating insects such as spruce budworm (Calhoun et al. 1992.). Several of these endophyte associations are also believed to be antagonistic to insect herbivores (Carroll 1991), although endophytes encompass a variety of ecological roles (Stone et al. 1994).

Endophyte species comprise an ecological assemblage that is distinct from saprophytic epiphytes and decomposers. Many are host specific or have restricted host distributions, but a few species with broad host ranges are often recovered from foliage at low frequencies. *Phyllosticta abietis* Bissett & Palm is the most common endophyte of *Abies* spp. in the Pacific Northwest, and also occurs on Douglas-fir. *Pleuoplaconema* sp., possibly the anamorph of *Chloroscypha chloromela* (Philips &Harkn.) Seaver, is the most common endophyte of *Sequoia sempervirens* (D.Don) Endl. (Espinosa-Garcia and Langenheim 1990, Rollinger and Langenheim 1993), and occurs as a dominant endophytic colonist throughout the natural range of the redwood (Rollinger and Langenheim 1993). *Rhabdocline parkeri* Sherw., Stone & Carroll, the most common foliar endophyte of Douglas-fir, is benign, but its congeners *R. pseudotsugae* Syd. and *R. weirii* Parker & Reid are defoliating pathogens of Douglas-fir (Sherwood-Pike et al. 1986). Several genera are recurrently isolated as endophytes from a variety of conifer hosts, including: *Phomopsis*, *Cryptosporiopsis*, *Cryptocline*, *Phyllosticta*, *Seiridium*, *Geniculisporium*, and *Nodulisporium*. Assemblages of foliar endophytes have been examined in several conifer hosts in the Pacific Northwest (Carroll and Carroll 1978; Petrini and Carroll 1981; Espinosa-Garcia and Langenheim 1990), and in the eastern United States (Bills and Polishook 1992).

Little is known of the details of colonization of foliage by endophytes. In species that have been studied, colonization is restricted to minute, limited portions of tissue in the epidermis or mesophyll. *Phyllosticta concentrica* Sacc. on *Taxus* spp. is apparently only subcuticular, whereas *P. abietis* on Douglas-fir and *Abies* spp. form limited intercellular infections within the mesophyll (Stone 1993). Infections of *Rhabdocline parkeri* are confined to single epidermal cells in healthy needles, but colonize extensively and sporulate on galls of the midge *Contarinia pseudotsugae* Condrashoff and also senescent and abscised needles (Sherwood-Pike et al. 1986; Stone 1987). Similar intracellular endophyte infections have also been observed for an unidentified endophyte in *Sequoia sempervirens* (J. K. Stone, unpublished). Endophyte infection densities and species richness increase with foliage age (Stone 1987; Espinosa-Garcia and Langenheim 1990). Douglas-fir needles are repeatedly infected by *R. parkeri* as they age (Stone 1987). Because *R. parkeri* occurs

as discreet, separate infection loci, the number of individual infections per needle can be counted and the total per tree estimated. McCutcheon et al. (1993) conservatively estimate the number of infections by *R. parkeri* in a single tree to be on the order of 10^{11}.

An endophytic habit similar to *R. parkeri* may be widespread in the Ascomycete family Hemiphacidiaceae. In the Pacific Northwest, *Didymascella thujina* (Durand) Maire, with its spotty distribution on dead needles on otherwise healthy branches of *Thuja*, is suspect; a better example would be *Fabrella tsugae* (Farl.) Kirschst. on eastern hemlock. This species can be reliably found in late winter on the oldest needles still attached to healthy hemlock trees; its appearance coincides with normal senescence. Most endophytes of conifers apparently cease growth soon after initial infection and remain quiescent until natural needle senescence or injury cause active growth to resume. These fungi have a competitive advantage in occupying foliage just prior to abscission, and are in a position to intercept translocated metabolites. As early colonists, they are also first in possession of the abscised needles and may be considered the first sere in the succession of decomposers (Stone 1987).

Bark endophytes

Many species of fungi colonize living bark on twigs and small branches of coniferous trees, but almost nothing is known of their biology. Resinous young bark of Douglas-fir generally supports *Arthopyrenia plumbaria* (Stitzenb. in Hasse) R. C. Harris and other non-lichenized members of the Arthopyreniaceae including *Mycoglaena subcoerulescens* (Nyl.) Höhn. (=*Winteria coerulea* (Ellis & Everh.) Berl & Voglino) and *Mycoglaena* sp. ("*Pseudoplea*"). *Arthopyrenia plumbaria* also occurs on red alder and other smooth-barked trees. In eastern North America, another non-lichenized member of a normally lichenized genus, *Arthonia impolita* (Hoffm.) Borrer, is ubiquitous on young bark of *Pinus strobus*. *Vestigium felicis* Piroz. & Shoem., an unusual coelomycete with "cat's paw" shaped conidia, is known only from young living twigs of *Thuja plicata* Donn ex D. Don in the Pacific Northwest (Pirozynski and Shoemaker 1972).

Ascomycetes that fruit on recently dead twigs still attached to otherwise healthy trees—notably, members of the Hypodermataceae, but also including *Lachnellula* spp. (Hyaloscyphaceae)—are prominent on living conifers in the Pacific Northwest. *Tryblidiopsis pinastri* (Pers.:Fr.) P. Karsten, a common circumboreal species which in our area occurs on *Picea engelmannii* Parry ex Engelm., and *Discocainia treleasei* (Sacc.) J. Reid & Funk, on *P. sitchensis* (Bong.) Carrière, are representative. Both fruit in abundance in the spring on twigs that have been dead for less than a year, and thus must be suspected of routinely colonizing bark of living twigs. Other species whose biology appears to be similar are *Therrya pini* (Albertini & Schwien.) Höhn. and *T. fückelii* (Rehm) Kujala on *Pinus* spp., *Coccomyces strobi* J. Reid & Cain on *P. strobus L.*, *Coccomyces heterophyllae* Funk on *Tsuga heterophylla* (Raf.) Sarg., and *Lachnellula ciliata* Dennis and *L. agasizii* (Berk. & Curtis) Dennis on *P. menziesii* and *Abies* spp., respectively. Live bark is apparently also the habitat of *Taxomyces andreanae* Strobel, Stierle, & Hess (Strobel et al. 1993), which has helped focus attention on the commercial potential of endophytes by virtue of its reported ability to produce the anticancer agent taxol *in vitro* (Stierle et al. 1993).

Bark endophytes, which then become the first successional species in the decomposition of dead branches (a process which in some conifer species proceeds to an advanced stage before the material falls to the forest floor), are potentially important in canopy ecology. Perhaps, for example, their presence excludes aggressive generalists that are actively pathogenic. On the other hand, all of the above species figure in lists of disease-causing fungi and can be found fruiting in abundance on diseased and dying trees, although generally (perhaps invariably) these trees are already severely weakened by other causes. The well-adapted parasite that is neutral or even beneficial under natural conditions can always become a serious problem in a stressed community, in artificial monoculture, when trees are introduced outside their normal range, and when closely related hosts from different parts of the world are brought into contact.

Xylotropic endophytes, fungi that are early colonists of sound wood, are another similar, apparently widespread group, although coniferous hosts from the Pacific Northwest apparently have not been examined for their presence. In Europe, healthy, attached branches of oak and beech

(Chapela and Boddy 1988; Boddy 1992), *Alnus* spp. (Fisher and Petrini 1990), and conifers (Sieber 1989; Kowalski and Kehr 1992), and in North America beech and aspen (Chapela 1989) are endophytically colonized by a mycobiota characteristic for each host (Chapela 1989). As with foliar endophytes, these fungi form disjunct, quiescent infections in healthy wood and resume active growth and eventually sporulate in response to drying of the substrate (Chapela 1989; Boddy 1992). Xylotropic and foliar endophytes have analogous life-history strategies that involve establishing early infections followed by a prolonged period of interrupted growth, which enables immediate invasion and saprophytic exploitation of the substrate at the onset of physiological stress or senescence. Facultative pathogens, such as *Hypoxylon mammatum* (Wahlenberg) J. H. Miller on aspen, as well as many wood decay fungi, are adapted to this strategy of early endophytic occupation.

Potential Sources of New Taxa

Colonists of Epiphytic Plants

Paradoxically, although the lichen flora of the Pacific Northwest is rich in terms of both species and biomass, lichenicolous fungi from the Pacific Northwest are underrepresented in the literature. This region has apparently not been systematically sampled or investigated, and only scattered collections exist. In Europe, for example, where lichenicolous ascomycetes have been more intensively studied, a rich and diverse mycobiota is known to be specifically associated with lichens (e.g. Hawksworth 1983). Judging from the relative ease of finding parasitised lichen thalli in our area, almost certainly a large reservoir of novel species or species not known from North America await discovery in the Pacific Northwest. Lichenicolous species are well represented in the Hypocreales and Dothideales and related mitosporic genera—orders that also contain numerous fungicolous species. Approximately ten genera of hyphomycetes and roughly an equal number of coelomycete genera are oligately lichenicolous (Hawksworth 1981). Recently, Diederich and Christiansen (1994) have identified the cause of galls common on *Usnea* spp. in the Pacific Northwest as an unusual Basidiomycete related to the Tremellales ("jelly fungi"). Other gall-like bodies on Lecanorales are also apparently caused by undescribed heterobasidiomycetes (Diederich 1990). Related lichenicolous *Tremella* spp. have been described (e.g., *T. coppinsii* Diederich & Marson on *Platismatia* spp.) and others are known to be mycoparasites of wood decomposing fungi, e.g., *Stereum*, *Peniophora* (Zugmaier et al. 1994). Some endemic species in the Pacific Northwest are *Lethariicola sipei* Grumm. on *Letharia* spp., and *Nanostictis pseudocyphellariae* Sherwood on *Pseudocyphellaria* spp. (Sherwood-Pike 1985, 1987). In addition to lichen parasites, fungal agents of in situ lichen decomposition comprise a distinct assemblage for which virtually no published information exists. Because of the specialized nature of the substrate, a highly adapted mycobiota associated with lichen decomposition is probable.

Epiphytic mosses and hepatics present another intriguing host association. Recently Weber (1995) has rediscovered *Selenospora guernisacii* (P. & H. Crouan) R. Heim & LeGal, an inconspicuous discomycete, associated with mosses in the Pacific Northwest. Döbbler (1979) has reported pyrenocarpous and pezizalean parasites of mosses in Europe. Hepatics, similarly, are known to form symbiotic intracellular associations with endophytic fungi (endomycothalli) in the gametophytes. Fungi belonging to Ascomycetes, Basidiomycetes, and Zygomycetes have been reported from these hosts, in a range of cytological specializations ranging from simple to complex (Pocock and Duckett 1985a,b). Arboreal mosses and hepatics may not harbor species distinct from the terrestrial habitat, but they represent a category of host well represented in mature conifer canopies, which almost certainly harbor a specialized mycobiota where new taxa might predictably be sought.

Canopy epiphytes also harbor several associated microscopic protozoa and small animals that are parasitized by specialized fungi. In recent years, discoveries of new taxa (genera and species) of fungal predators and parasites of rotifers, amoebae, nematodes, tardigrades, springtails, and other organisms have flourished. Most habitats where these animals exist, e.g. moss, rotting wood, leaf mold, have also yielded new and interesting fungal predators and parasites (Drechsler 1944; Barron 1981, 1991; Barron et al. 1990; Barron and Szijarto 1990), although relatively few groups are working on them worldwide. Ascomycetes, Basidiomycetes, Zygomycetes, and Oomycetes are represented in predators and parasites of protozoa and small animals. These fungi display an aston-

ishing degree of specialized adaptations for capture and penetration of prey species, and constitute one of the better examples of adaptive radiation in the fungi. A number of *Nematoctonus* anamorphs of Hymenomycetes such as *Hohenbuehelia* and *Pleurotus* are known to form traps for capturing nematodes (Thorn and Barron 1984), presumably an adaptation of cellulose decomposers to the low nitrogen content of the substrate (Barron 1992). Again, careful examination of canopy habitats is almost certain to add novel taxa in this group.

Interactions with Canopy Arthropods

Coniferous canopies in the Pacific Northwest are rich in arthropod species. Voegtlin (1982) reported approximately 1500 taxa from the canopies of old-growth Douglas-fir, and concluded that Douglas-fir canopies supported the greatest diversity of arthropods of any canopy system studied to date. Few of the species reported were endemic, i.e. having their entire life cycle completed in the canopy; those that are endemic are primarily mites, Collembola, and Psocoptera. The literature on arthropod—fungus interactions is enormous and beyond the scope of this paper to review, but we should at least point out that the propensity for fungi to form complex, specialized associations with insects is ancient and fundamental. Detailed reviews of fungus—arthropod interactions can be found in Batra (1979) and Wheeler and Blackwell (1984). Again, unfortunately, published information specific to the canopy habitat is almost completely lacking.

It is almost axiomatic that wherever a high degree of arthropod diversity exists, a corresponding diversity of associated fungi will be found, although many of the fungal groups that form close symbioses with insects are among the poorest documented taxonomically. The Laboulbeniales, for example, is an order of obligate ectoparasites of insects and mites and spiders (reviewed by Weir and Beakes 1995). While many genera and species of Laboulbeniales have broad host distributions, a few species have sex- and even positional specificity (Benjamin 1971). Although the Laboulbeniales, with around 2000 species, is one of the most speciose orders of Ascomycetes and is probably the largest and most highly specialized group of entomogenous fungi, only a fraction of the potential hosts have been examined, and thus the number of undescribed species is a matter of conjecture. The Trichomycetes, a similarly neglected group of Zygomycetes, are obligate commensals or parasites found in the digestive tracts of arthropods (Moss 1979). An example of insect-fungus interaction more typical of treetops is that between the woodboring Scolytid beetles, which actively cultivate and are nutritionally dependent upon "ambrosia fungi," a diverse assemblage of anamophic Ascomycetes. The beetles have specialized anatomical structures (mycangia) for establishing new fungal cultures when a new woody substrate is invaded (Norris 1979). Vectoring of pathogenic fungi by insects is one of the better understood and most ecologically important fungus-insect interactions involving forest trees, for example vectoring Ophiostomatoid fungi by *Dendroctonus* and *Scolytus* beetles (see Harrington, 1993; Malloch and Blackwell, 1993).

Aquatic Hyphomycetes in Lodged Litter

Conidia of aquatic hyphomycetes, mitosporic fungi with tetraradiate or sigmoid conidia specialized for aquatic dispersal, are typically associated with senescent and decaying leaf litter from trees growing near rapidly flowing streams (Webster 1981). Conidia characteristic of these fungi also are commonly recovered from rainfall samples collected beneath mature canopies from upland sites far from streams in Oregon (G. C. Carroll, unpublished). Sigmoid, helicoid, tetraradiate, and branched conidia representing several anamorph genera, have been collected from rainwashed trunks of several tree species in the Pacific Northwest (Bandoni 1981). While many of the conidia thus collected can be readily assigned to existing genera and species, e.g. *Gyoerffella biappendiculata* (Arnold) Ingold, apparently undescribed taxa are not uncommon in rainfall samples. Different species seem to occur in association with different host trees, but the source of the conidia and the ecological role of these fungi in the canopy remains enigmatic. Lodged leaves and debris are a probable source. Ando (1992) has shown that some "terrestrial aquatic hyphomycetes" are endophytic leaf colonists or parasites that sporulate ephemerally in surface condensation of leaves.

Fungi on Standing Dead Wood

Depending on the species, coniferous trees may support a large volume of dead branches in the canopy, particularly at high elevations. This aerial

niche supports a diverse assemblage of unusual fungi, whose adaptations and taxonomic diversity have been discussed in detail by Sherwood (1981). Three species predominate on standing dead coniferous wood at high elevations; *Agyrium rufum* (Pers.) Fr., an unusual non-lichenized member of the Lecanorales whose closest relatives are resinicolous fungi, also occurring on living conifers; *Xylopezia hemisphaerica* (Fr.) Höhn., a taxonomically isolated loculoascomycete, and *Cryptodiscus pallidus* (Pers.:Fr.) Corda (Ostropales). Also common in this habitat are *Durella atrocyanea* (Fr.) Höhn., *Propolis* spp., *Melittosporium propolidioides* (Rehm) Rehm, *Stictis* spp., *Mycocalicium* spp., and Odontotremataceae. This habitat is unusually rich in taxa (genera and families) that include both lichenized and non-lichenized species. Basidiomycetes are not prominent in the known mycobiota on small standing dead-woody coniferous material in the Pacific Northwest. It seems improbable that Basidiomycetes are actually as little represented in nature as our present knowledge suggests. At high elevations and drier areas aerial decomposition is clearly a lengthy process providing a stable niche with considerable spatial and temporal differentiation.

Specificity to old-growth?

Many of the species included in this discussion are known from only a few collections, so that any generalizations about their specificity to undisturbed sites must necessarily be speculative. Clearly, a host-specific fungus growing only on a rare species confined to undisturbed sites is threatened if its host is threatened. The importance of leaving some proportion of dead wood in managed forests is increasingly recognized, which should have a positive effect on preserving uncommon species of lignicolous fungi. Most of the fungus species mentioned also occur in mature second growth within the normal geographic range of the host species.

Besides the possibility of harboring unique microfungal species, old-growth stands and individual trees may also represent a large reservoir of infraspecific genotypic diversity. McCutcheon et al. (1993) provide evidence that the foliage of old-growth trees supports a large diversity of genotypes of the endophyte *Rhabdocline parkeri,* and showed that the number of unique genotypes of *R. parkeri* infecting young trees in managed stands in close proximity to old-growth stands was similar to that of the old-growth trees but much greater than in managed stands of similar age farther away from old-growth trees. A tree from an isolated site had the fewest *R. parkeri* strains. For microfungi such as *R. parkeri,* old-growth trees represent an archive of genetic diversity. Carroll (1988) has suggested that genotypic diversity of an endophyte may help confer acquired resistance against herbivorous insects to the host tree through the combined activity of a variety of antagonistic metabolites produced by the fungus. The canopy microfungi of isolated trees, urban plantings, and trees growing outside their normal range is quite different from that occurring naturally.

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Death and Decay: A Vital Part of Living Canopies

Abstract

Wood decay is a significant ecological process affecting Northwest forest canopies. Standing dead trees (snags) and partially decayed living trees offer five primary functions in the forest canopy: they increase structural diversity, alter canopy microenvironment, promote biological diversity, provide critical habitat for wildlife, and act as storehouses for nutrient and organic matter recycling agents. In this paper we do not discuss traditional measurement of wood decay in the canopy as a silvicultural loss of standing timber, but review current literature of forest ecology and define wood of dying and dead trees as an important component of the aboveground ecosystem.

Introduction

In the last two decades, considerable research has helped elucidate the role of "dead and down" wood in forest ecosystems (Graham and Cromack 1982, Erickson et al. 1985, Harmon et al. 1986, Sollins et al. 1987, Means et al. 1992). Earlier, in his classic pioneering work on the subject, *The Pattern of Animal Communities*, Charles Elton stated that the wood of dying and dead trees provides one of the greatest resources for animal species in natural forests (Elton 1966). In temperate forests, Elton estimated if fallen timber and slightly decayed trees are removed from the system "the whole system is gravely impoverished of perhaps more than a fifth of its fauna." Although insightful for the era, Elton's appraisal of the importance for this ecosystem component likely falls short. Even with our current understanding of ecosystem function, we cannot adequately assess consequences to the system of having decayed and dead trees removed or not available (i.e., through several forms of forest management).

The wood of dying and dead trees helps to vary the pattern of forest communities, not only on the ground but also at all levels of the canopy. Many organisms share dependence on the wood of dying and dead trees, but little is known of their inter-dependence and how they interact within the larger system. The general stages by which standing timber is invaded by insects and fungi are well known from the extensive work of forest entomologists, pathologists, and mycologists, but little effort has been applied to clarifying the ecosystem function of the standing dead. Research efforts presumably have been hindered not only by the difficulty of safely working in standing decaying trees, but by the inherent complexity of the effects. Generally, ecologists have underestimated that the way trees die can markedly influence several ecological processes.

Decay of a tree progresses until, ultimately, its residues are fully integrated into the soil. Standing dead trees may be susceptible to windthrow, which uproots the tree, or to bole breakage close to the ground that prostrates the entire bole. Just as frequently, much of the decay process takes place while the tree is standing and an integral part of the living canopy (Graham and Cromack 1982). Living trees with partial decay may remain upright for decades, their dead, decaying branches intermingling with living branches (Figure 1).

Distribution and Causes of Dead Wood in the Canopy

Much of the decayed wood in canopies is within the main bole and stems of live trees. This "heartrot" can account for 20% or more of the total volume of wood in a stand of trees. As a function of stand age, older stands have more decay as a total percentage of the volume (Childs and Shea 1967, Aho 1977). When estimating for timber production, a measure of annual volume growth increment is calculated; from that amount is

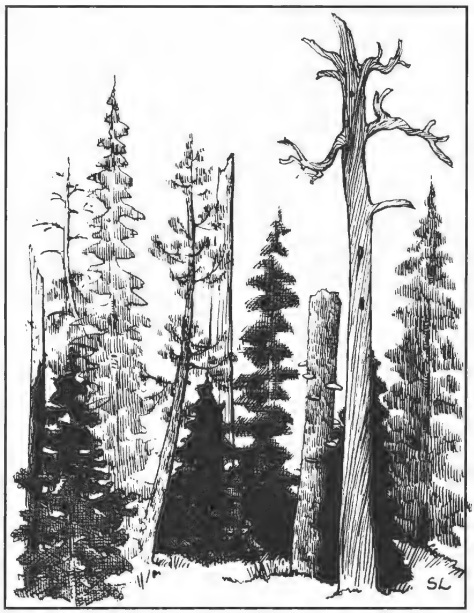

Figure 1. Dead boles and branchees are an integral part of the living canopy.

subtracted the increasing increment of defect caused by heartrot fungi to get a realistic estimate of volume growth. At some point in the life of trees the increment produced by annual growth equals the amount of wood destroyed by heartrot fungi. This point is a theoretical age of maximum volume of merchantable wood. It is referred to as the "pathological rotation age" (Manion 1981). For obvious reasons, the timber producers aim to harvest the stand long before this point is reached. Intensive management involving even-aged, short-term rotations, harvests trees while wood decay in the canopy is minimal.

Dead wood is not randomly distributed across the forest canopy. Incidence of wood decay has been correlated with stand age, climatic zones (Setliff 1986), elevation and soil type (Hobbs and Partridge 1979), and habitat type (Byler et al. 1990). Some disturbance agents may cause wide-scale mortality throughout a forest landscape, but certain insects, parasitic plants, and root and stem fungi affect patches of trees and exhibit spatial patterns that are aggregated or clumped in the forest canopy (Knight 1987, Geils 1992).

Fire may be a major contributor to subsequent canopy tree decay. Trees are fire-killed directly by stem girdling, crown scorching, and burning of the root systems. Trees can be fire-killed indirectly through basal wounds. Wounding events such as fire scars, broken tops, or other stem injuries create infection courts for stem- and root-decay organisms. Trees respond to wounding and infection by compartmentalizing the infection and wounds, which can result in hollow or soft inner cores and hard outer shells after many years. This "hard outer shell and soft core" is critically important to cavity-nesting vertebrates. This process of compartmentalization helps trees limit wood decay (Shigo and Marx 1977).

Wood-boring arthropods also may initiate the decay process or act as secondary agents of decay. Repeated defoliation of conifers can cause mortality, or weaken trees and allow successful attack by secondary bark beetles (Wickman 1978). Healthy trees also can be killed by insects that came from adjacent trees killed by fire, insects, or root diseases (Furniss 1936, Childs 1960).

Perpetual natural thinning of trees growing in subordinant canopy positions is known as suppression mortality. Natural senescence of all sizes of branches, especially in mature trees, translates to a large biomass of dead and decaying wood located in the canopy (Pike et al. 1977).

The Decomposer Community

Wood is a bulky, spatially determinate resource that decomposes slowly relative to most plant litter; it takes on average 15-20 years for small (>5-cm diameter) branches and over 300 years for large trunks to decay in temperate forests (Boddy 1992). As wood decay organisms colonize and use wood they encounter continually changing conditions, *e.g.* an increase of porosity, decrease of apparent density, and so forth. The changes may, in turn, affect the activity and development of the decomposer community (Yoneda 1975).

Dying and dead wood in the canopy is broken-down by the combined action of the decomposer community, which is composed predominately of micro-organisms (bacteria and fungi) and invertebrate animals (Käärik 1974, Swift 1977). These organisms "feed" on the dead wood, using its carbon, and other nutrients for their own growth and development. Eventually the decomposers die, their carcasses become integrated with the dead wood, and they are acted upon by other decomposers.

As with successional changes in seed plant communities, directional trends in the decomposer community are associated with wood decay in forest canopies (Hudson 1968, Blanchette and Shaw 1978). Much is known of the substratum succession of decay organisms in the dead and down tree (Swift 1982a, Swift 1982b, Harmon et al. 1986), but the studies of decay organism succession in canopy wood has lagged far behind.

Five Primary Functions of Decaying and Dead Trees in Forest Canopies

Five primary functions of aboveground decaying wood in the forest system are to increase structural diversity, alter canopy microenvironment, promote biological diversity, provide critical habitat for wildlife, and act as a storehouse for nutrient and organic matter recycling agents. These functions are highly correlated with complex interactions but will be discussed separately in the following text.

Increase Structural Diversity

The structure provided by boles and branches of trees that are dead, decaying, or both is a distinctive and dynamic feature of the canopy (Figure 2). Stand structure is altered by canopy gaps caused by the partial or complete mortality of an individual tree or group of trees.

The lag time between tree death and the onset of fragmentation is influenced by species, size, microclimate, and type of mortality (Harmon et al. 1986). Lag times for snags to begin falling are reported to be <3 years (Harmon et al. 1986). Hennon et al. (1984, 1990) found that some Alaska-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach) snags were persistent in forest canopies of southeastern Alaska for over 100 years.

Decay of boles differs from that of small branches and twigs. The bole is a denser substrate and is likely to house a different community of organisms than the fine twigs and small branches, which are less dense and have a greater surface

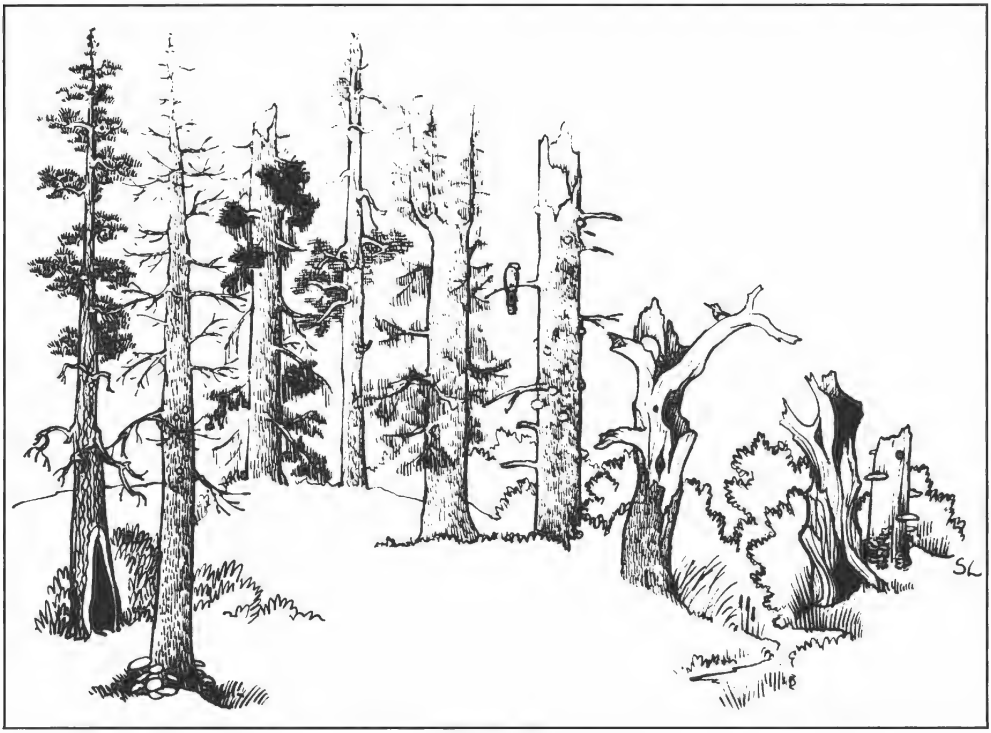

Figure 2. Various stages of tree decay provide dynamic diversity in canopy structure

area than the wood of the bole. Most studies of canopy biomass seem to ignore the dead wood component—either ignore that it is dead or simply omit dead branches from the sample. In one old-growth stand (>400 years), the biomass of dead twigs in the canopy of living trees was equal to roughly 18% of the total twig biomass and about one-third of the needle biomass (Pike et al. 1977). Even more surprising, dead twigs represented 47% of the total twig surface area.

Alter Canopy Microenvironment

The microenvironment within the vertical profile of the canopy is controlled to a large degree by the structure of the canopy. Death of whole or partial tree crowns plays an important role in defining the nature of that structure. Gaps in the living canopy also alter its structure by varying the patterns of light, moisture, wind, and thermal properties (Oliver and Stephens 1977, Oliver and Larson 1990). These gaps also increase the heterogeneity or "roughness" of the upper canopy, which creates a broader gradient of light, temperature, and humidity. In rough, deep, canopies of older forests in the Pacific Northwest the diverse forest microclimate is reflected in the vertical distribution of epiphytes (McCune 1993).

Patches of dead trees within old-growth stands provide habitat for wildlife that require grass-forb or shrub conditions for reproduction and feeding. Immense tree mortality may be disadvantageous to deer and elk, however, because of loss of canopy cover traits. Under full canopy cover, the animals are less subject to extremes in temperature, solar radiation, windspeed, humidity, rain throughfall, snow accumulation, predation, and human disturbance (Witmer et al. 1985).

Promote Biological Diversity

Dead and decaying wood provides an exceptional environment in the forest canopy. On a stand scale, even small modifications to canopy structure may allow previously nonresident species to grow and occupy a niche. On a smaller scale, the special microenvironment caused by dead and decaying wood contributes to the life support system for many canopy-dwelling microorganisms, invertebrates, birds, mammals, and plants.

Wood-attacking fungi are mainly basidiomycetes (Hawksworth et al. 1983), although some ascomycetes and other fungi may be present and attack cellulose or other substrates (Hudson 1968). Although fungi act as the main agents of wood decomposition, other organisms also use rotting wood. These include bacteria, yeasts, myxomycetes, and invertebrates, particularly insects but also oligochaetes, mites, and nematodes (Harmon et al. 1986). Their major influence is in interacting with mycelial fungi, which can alter community structure, community dynamics, and rates of decay. These interactions may be direct, as with grazing of fungal mycelium, antibiosis, and nutrient competition, or indirect, by operating through alterations to the wood substratum and microclimate (Boddy 1983).

Invertebrate use of and dependence on canopy dead-wood is well known to entomologists. By chewing, ingesting, and excavating, invertebrates create a dust that decays more rapidly than the original wood because of an increased surface-to-volume ratio (Ausmus 1977, Harmon et al. 1986). Depending on the species, invertebrates either transport these particles from the wood or leave them inside. The galleries made by invertebrates allow microbes to colonize dead wood more rapidly (Ausmus 1977, Swift 1982a). Some invertebrates are fungivorous, and the decomposer fungi produce abundant resources for grazing. Furthermore, invertebrates are an important food source for vertebrates, such as bears and birds, that fragment the material while foraging (Almack 1985, Beckwith and Bull 1985).

In the Pacific Northwest, more than one hundred species of wildlife depend on snags for habitat (Thomas et al. 1979, Neitro et al. 1985). The listing includes representatives from all classes of terrestrial animals. The dependency of these species on trees that are dead, decaying, or both ranges from absolute to incidental, but for some species the presence of dead trees can spell the difference between local extinction and the perpetuation of existing populations (Thomas et al. 1979, Neitro et al. 1985).

Dead wood also provides a unique canopy substrate for plants. For example, some lichens are associated almost exclusively with dead trees or branches in the canopy. Members of the "pin lichens," in particular, are most often found using dead, bare wood versus bark as structural habitat. Once this wood fragments and falls to the forest floor, the lichens fail to thrive under the new environmental conditions and die (B. McCune, Oregon State University, pers. comm.).

Stephen Sillett (Oregon State University, pers. comm.) has observed dead wood in giant sequoia (*Sequoiadendron gigantea* (Lindl.) Buchholz.) acting as a stable substrate for epiphytes. Giant sequoia has a bark that characteristically sheds and flakes. In his survey of sequoia for epiphytes, dead wood and old persistent seed-cones were the primary areas where epiphytes were growing.

Provide Critical Habitat for Wildlife

As wildlife habitat, dead and dying trees function in a variety of ways (Table 1). Decaying wood is particularly important to cavity-nesting birds because wood decay in stems is an essential precursor to use by cavity excavators (McClelland and Frissell 1975, Cline et al. 1980). Large trees that contain heartrot before they die may be particularly important because they may be used by primary excavators before and long after tree death (Hennon and Loopstra 1991).

Recent findings by Akenson and Henjum (1994) suggest that black bear in the Blue Mountains of Oregon are intimately associated with canopy wood decay. They report that of 23 den sites used by radio-instrumented bears, 20 are tree-associated. Among these, 10 are top entry into hollow centers. All 10 trees are standing and 6 are living. The internal cavities within these trees resulted from stem decay by fungi.

In the past, in intensively managed forests of the Pacific Northwest, most snags were cut to reduce safety and fire hazards, and to increase the yield of woody fiber (Woodfin 1976). Current recommendations (USDA Forest Service R6, amendments to Forest Plans, 1994) for managed forests include a broader approach to habitat management for dead-wood-dependent wildlife that retains snags and other woody debris.

Act as Storehouses for Nutrient and Organic Matter Recycling Agents

The notion that down woody debris improves long-term site productivity by enhancing the nutrient capital, water economy, and soil organic reserves is well documented (Franklin and Waring 1980, Maser and Trappe 1984). The concept that the decomposition process is often initiated and dependent on conditions in the canopy zone before the fall of the material is often ignored.

The role of decay within standing trees associated with cycling of nitrogen (N) is particularly interesting from an ecosystem perspective. In the short-term, decaying trees may be a nutrient sink, but over the long run they are a source of nutrients (Harmon et al. 1986). For example, Harvey et al. (1989) reported that N-fixing bacteria populations accompany common fungal-initiated wood decay processes in living trees. Nitrogen fixation was demonstrated in decay columns caused by various fungi in several western conifers. They used these data to approximate the nitrogen fixation potential in the forest ecosystems of northern Idaho. Their calculations propose that the N gains in decaying, live trees on northern Idaho sites amount to between 0.06 and 4.91 kg/ha per year and primarily depend on volume of decay in live standing trees on site. Such large N gains on some sites could equal or surpass the amounts of N fixed in downed woody residues on forest soils in the northern Idaho region (Jurgensen et al. 1989).

Wood decay fungi can be grouped into two categories according to the way in which they decay wood. These two groups are referred to as white rot fungi and brown rot fungi. White rot fungi have cellulase and lignase enzyme systems that enable them to degrade all components of woody cell walls. Most of these fungi apparently remove the lignin and polysaccharides at about the same rate (Gilbertson and Ryvarden 1986). White rot fungi eventually decay wood completely, and white rot residues are not stable components of forest soils.

Brown rot fungi selectively remove cellulose and hemicellulose from wood. In advanced stages, wood is reduced to a residue of amorphous, crumbly, brown cubical chunks composed largely of only slightly modified lignin. Brown rot residues are extremely stable and are major organic components in forest soil (Gilbertson and Ryvarden 1986).

Both white and brown rot fungi decay wood in the canopy zone (Hepting 1971). Brown rot fungi may be particularly important organisms in forest ecosystems of the Pacific Northwest. Considering all wood-decaying fungi, species of brown rot fungi are relatively few when compared to numbers of species of white rot fungi (only about 7%) (Gilbertson and Ryvarden 1986). Brown rot fungi occur primarily on conifer wood. On a geographic basis, brown rot fungi are primarily distributed in coniferous forest ecosystems. Gilbertson and Ryvarden (1986) suggested that because fossil records indicate brown rot fungi

TABLE 1. Some uses of snags by selected wildlife species (as modified from Neitro et al. 1985)

Use	Pileated woodpecker	Red-breasted sapsucker	Acorn woodpecker	Turkey vulture	Owls and raptors	Osprey	Bald eagle	Flycatchers	Brown creeper	Bats	Raccoon and black bear	Small mammals
Cavity nest sites	X	X	X		X							X
Nesting Platforms						X	X					
Feeding substrate	X	X	X						X			
Plucking posts					X							
Singing or drumming (communication)	X	X	X									
Food cache or granary			X									X
Location of courtship	X	X	X									
Overwintering sites	X		X		X					X	X	X
Roosting	X	X	X	X	X	X	X			X		
Lookout posts				X	X	X	X	X				
Hunting and hawking perch					X	X	X	X				
Fledgling site						X	X					
Dwelling or dens											X	X
Loafing sites				X		X	X					
Nesting under bark									X			
Communal nesting or nursery colonies			X							X		
Anvil sites			X									
Thermally regulated habitat	X	X	X		X					X		X

were present about 300 million years ago during the carboniferous age when the development of woody gymnosperms began, brown rot fungi evolved along with conifers and probably played an important ecological role in the evolution of coniferous forest ecosystems.

We know that, on the forest floor, brown rot residues remain essentially unaltered in the soil for hundreds of years. They may comprise up to 30% of soil volume in the upper layers, are major sites of ectomycorrhizal development and nonsymbiotic nitrogen fixation, may increase the

water-holding capacity of the soil, ameliorate soil temperatures, and increase the soil cation exchange capacity (Gilbertson and Ryvarden 1986). The extent of specialized roles that brown rot fungi may play in the canopy zone is largely unknown.

Conclusions

Death and decay of woody components of tree crowns, including heartrot of living stems, dead branches, and dead trees, are important, functional aspects of forest canopies that have been largely ignored in forest canopy studies because of the difficulty of access and quantification. Generally, ecologists have underestimated that the way trees die can markedly influence numerous ecological processes. Most study of this important resource has been by wildlife biologists interested in habitat associations, and by forest pathologists interested in reducing losses of timber value. In no way do we intend to question the need to reduce losses of timber volume in forest plantations where economy is the driving factor; we only want to elucidate the importance and functional aspects of decaying and dead trees in the forest canopy because we believe it is critical and not well understood. Canopy studies must include decaying and dead trees as subcomponents of the ecosystem if we are to more thoroughly understand what is occurring aboveground.

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Emerging Themes in Epiphyte Research in Westside Forests with Special Reference to Cyanolichens

Abstract

Canopy epiphyte research in the Pacific Northwest has entered its third decade, and three basic patterns of epiphyte distribution are now known. First, epiphyte biomass and diversity slowly increase during forest succession. This trend is most obvious with cyanolichens, which dominate epiphyte communities in old-growth forests but are scarce in younger forests. Second, epiphyte functional groups seem to migrate upwards in the forest canopy during succession. In the oldest and wettest forests, bryophytes come to dominate epiphyte communities, and several species of terrestrial plants actually grow on branches in the upper canopy. Third, cyanolichens are most abundant in old-growth forests on lower slopes. They are scarce in similar forests located farther upslope away from streams. Causes of these three patterns are not clearly understood, but they have important consequences for epiphyte recovery in managed forests.

Introduction

Epiphytic lichens and bryophytes are a conspicuous and ecologically significant component of westside forests in the Pacific Northwest, where their biomass can exceed three tons per hectare (McCune 1993, Neitlich 1993). These epiphytes can be divided into four functional groups based on their ecological roles: cyanolichens, 'alectorioid' or forage lichens, 'other' lichens, and bryophytes (McCune 1993). Cyanolichens, or nitrogen-fixing lichens, are the dominant epiphytes in old-growth forests where they constitute over half of the total epiphyte biomass (Pike et al. 1977, Rhoades 1981, McCune 1993, Neitlich 1993). They fix large quantities of atmospheric nitrogen (Pike 1978), making it available for plant uptake. Nitrogen-rich leachates from these lichens also serve as a base for complex food webs in the forest canopy (Carroll 1979). Epiphytes have other important functions in forest ecosystems, such as providing critical winter forage for mammals, serving as food and habitat for invertebrates, and providing nesting material for birds (Slack 1988, Rhoades 1994).

A considerable amount of canopy epiphyte research has occurred in westside forests during the last two decades. Early studies documented the floristic composition of the old-growth forest canopy (Denison 1973, Pike et al. 1975) and quantified epiphyte biomass in selected tree crowns (Pike et al. 1977, Rhoades 1981). Recently, McCune (1993) proposed the *similar gradient hypothesis* which provides a framework for understanding the distribution of epiphytes in westside forests. According to this hypothesis, "epiphyte species are ordered similarly on three distinct spatial and temporal gradients. These gradients are 1) *vertical* differences in species composition in a given stand, 2) species compositional differences among stands differing in *moisture* regime but of the same age, and 3) changes in species composition *through time* in a given stand" (McCune 1993). Although, empirical support for McCune's hypothesis is currently insufficient to fully test it, the evidence is growing, especially for cyanolichens.

Our purpose in this article is to highlight three major patterns which have emerged from recent studies of epiphytes in westside forests: the slow development of epiphyte communities during forest succession, the apparent upward migration of epiphyte functional groups over time, and the riparian influence on epiphyte distribution. McCune's similar gradient hypothesis provides a framework for the discussion. This paper focuses on several key studies of epiphytes in forests of the Coast and western Cascade Ranges, drawing on both personal observations and preliminary results from ongoing studies. We conclude with a brief discussion of research approaches and some suggestions for future research that will have implications for forest management.

Slow Development of Epiphyte Communities

Studies in Europe (Rose 1992), Montana (Lesica et al. 1991), and Oregon (Neitlich 1993) have dem-

onstrated that old-growth forests support far more diverse and abundant epiphyte communities than do younger forests. In westside Douglas-fir forests of the Pacific Northwest, the most striking difference between epiphyte communities of old-growth forests and younger forests is in cyanolichens, which dominate the old-growth canopy (Pike et al. 1975) but are scarce or absent in younger forests (Figure 1). Several epiphytic cyanolichen species are seldom found in forests less than a century old (Table 1, Holthausen et al. 1994). The reasons for this slow development of epiphyte communities during forest succession are not entirely clear. Possible explanations include dispersal limitations, unsuitable substrates, and/or unsuitable canopy microclimates in younger forests.

Dispersal limitations appear to be important in certain cases. The effects of dispersal limitations can be most readily observed when barriers to dispersal are removed. For example, late successional epiphytes can become abundant in a young forest growing within 10 m of an old-growth forest edge even though they are scarce in the interior of the young forest. Many of these species might be capable of long-distance dipersal via spores, tiny asexual propagules, or both, and their complete absence from younger forests is not to be expected unless suitable substrates or microclimates are lacking in younger forests. Long-term studies involving inoculations of bark surfaces with epiphyte propagules are needed to determine if dispersal is a major factor limiting epiphyte colonization of tree crowns.

Support for substrate limitation as a factor contributing to epiphytic differences bewteen old and young forests comes from a recent study in Glacier Bay, Alaska (Neitlich & Campbell, unpublished). Cyanolichen species richness was considerably higher on *Alnus sinuata* than *Picea sitchensis* in young stands, whereas 200-year-old *Picea* trees harbored a richness similar to that found in *Alnus* trees one hundred years younger (Figure 2). In some conifer forests of western Oregon, a similar phenomenon seems to occur on *Acer, Fraxinus,* and *Quercus* instead of *Alnus.* Perhaps the smooth bark of young conifers is less likely to retain epiphyte propagules than the rougher bark of older trees or hardwoods (Armstrong 1990). Alternatively, bark chemistry, crown architecture, and/or light environment may account for differences in epiphyte communities between conifers

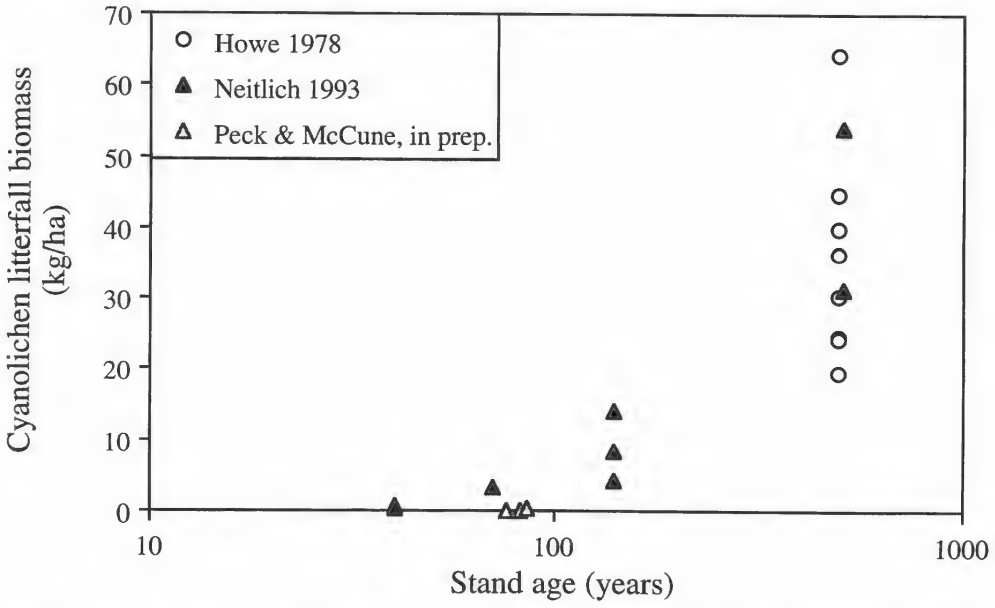

Figure 1. The relationship between epiphytic cyanolichen biomass and stand age for 19 forest stands in the central western Oregon Cascades. All stands were below 900 m elevation, less than 100 m above a major stream, and dominated by Douglas-fir. The x-axis is on a log scale. Data from Howe (1978), Neitlich (1993), and Peck & McCune, in prep.

TABLE 1. Rare epiphytic cyanolichen species associated with late-successional and old-growth coniferous forests in the Pacific Northwest. A dagger (†) signifies species endemic to the Pacific Northwest of North America.

Species	Occurrence	Notes
Dendriscocaulon intricatulum	3, 16, 17	extremely rare
Lobaria linita	1, 3, 4, 7, 11, 16, 17, 18, 19	mostly on rock at high elevations in CA, OR, and WA; also epiphytic at low elevations in AK, rarely south to OR and WA
Nephroma occultum†	3, 4, 16, 17	middle to upper canopy in OR and WA; occurs lower in canopy in BC and AK
Nephroma silvae-veteris†	3, 4, 16	middle canopy
Pannaria rubiginosa	2, 3, 4, 11, 16	lower to middle elevation forests
Pseudocyphellaria sp. (close to *P. aurata*)	4, 14	primarily coastal; known from 4 collections, all in OR
Pseudocyphellaria rainierensis†	1, 3, 4, 7, 16, 17	lower canopy and understory
Sticta weigelii	1, 3, 4, 7, 16	lower to middle canopy and understory
Sticta wrightii	16, 17	extremely rare

Occurrence Codes:

1. Olympic Peninsula
2. Western Washington Lowlands
3. Western Washington Cascades
4. Western Oregon Cascades
5. Eastern Washington
6. Eastern Oregon Cascades
7. Oregon Coast Range
8. Willamette Valley
9. Oregon Klamath
10. California Klamath
11. California Coast Range
12. California Cascades
13. California Coast
14. Oregon Coast
15. Washington Coast
16. British Columbia
17. Southeast Alaska
18. Idaho
19. Montana

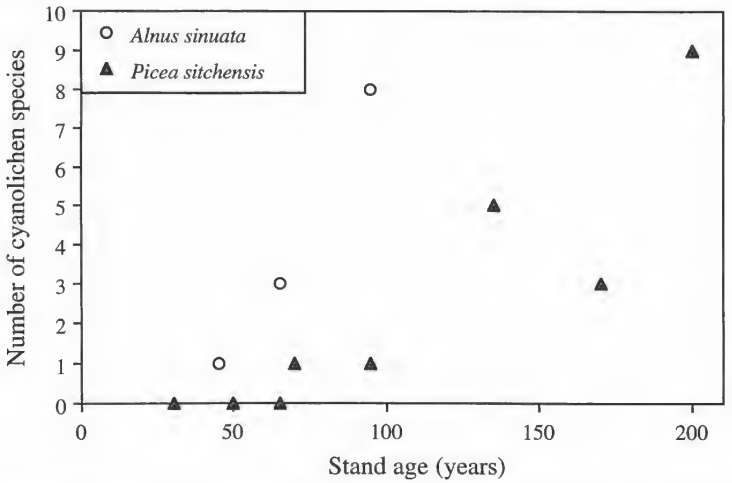

Figure 2. The effect of forest age on cyanolichen species richness on two tree species in spruce forests of Glacier Bay, Alaska. Total number of cyanolichen species are presented for each tree species in each site where they were found in the chronosequence. Tree species in each site were surveyed until four trees were climbed with no additional lichen species encountered. Data from Neitlich & Campbell, unpublished.

and hardwoods (Hyvärinen et al. 1992). Controlled studies of epiphyte establishment on a wide range of bark substrates available in westside forests are greatly needed. The potential of hardwood retention as a means of boosting epiphyte species diversity in managed forests is a promising area for future research.

A third impediment to epiphyte community development in young forests may be unsuitable canopy microclimates. Young, even-aged forest canopies are very shaded and sheltered from direct precipitation in contrast to the more open and structurally complex old-growth forest canopy (see Ch. 6, Geiger 1965). Thus, low moisture and light availability in young, managed forests may limit the growth of some canopy epiphytes (Rose 1992). The idea that the suitability of epiphytic habitats in a forest canopy improves during succession is compelling, but so far no studies have demonstrated such an effect. Documentation of the micrometeorological basis for this effect (*i.e.*, light and humidity regimes) requires an enormous and costly effort. Experiments involving transplanting epiphytes in tree crowns (*e.g.*, Sillett 1994, 1995a) are a reasonable alternative in which growth rates provide a relative measure of epiphyte habitat suitablity in forests of different ages.

Upward Migration of Epiphyte Functional Groups

McCune (1993) described an apparent upward migration of epiphyte functional groups in forest canopies over time: 'other' and 'alectorioid' lichens are the first epiphytes to colonize young forests, but they are steadily displaced upwards in tree crowns by cyanolichens and bryophytes, which come to dominate the lower forest canopy. The oldest forest included in McCune's study was just over 400 years. Does this upward migration continue? A recent study of a 700-year-old Douglas-fir forest suggests it does. In this stand (described in Sillett 1995b), cyanolichens and bryophytes, especially *Antitrichia curtipendula,* were abundant throughout the forest profile. Several cyanolichen species normally found in the understory of 450-year-old Douglas-fir forests (*e.g., Pseudocyphellaria rainierensis,* Pike et al. 1975) were widely distributed in the lower to middle crowns of the large Douglas-fir trees in this stand. Similarly, in the oldest, wettest forests of the Pacific Northwest, such as those found in the true rainforests of Mount Rainier and Olympic National Parks, Washington, as well as parts of Vancouver Island and southeast Alaska, the upward migration of epiphytes appears to have progressed to its limit—an almost complete domination of the canopy by bryophytes. In fact, many terrestrial species of mosses and vascular plants have been observed growing on branches in the upper canopies of these forests (Table 2). Factors controlling the rates of upward migration of epiphytes are not understood, although bryophyte domination of the canopy appears to be most rapid in very wet coastal forests.

TABLE 2. Examples of terrestrial plants occasionally found as epiphytes in the upper canopy of the oldest and wettest Douglas-fir forests in the Pacific Northwest.

Vascular plants	Mosses
Epilobium angustifolium	*Eurhynchium oreganum*
Gaultheria shallon	*Hylocomium splendens*
Oplopanax horridum	*Isopterygium pulchellum*
Sambucus racemosa	*Mnium spinulosum*
Tsuga heterophylla	*Polytrichum juniperinum*
Vaccinium spp.	*Rhytidiadelphus loreus*
	Rhytidiadelphus triquetrus

The Riparian Influence on Epiphyte Distribution

Cyanolichen biomass in westside forests depends not only on stand age but also on landscape position. For example, old-growth Douglas-fir forests close to major streams support a far greater cyanolichen biomass than comparable upland forests (Howe 1978, Figure 3). The cause of this pattern is not entirely understood. Perhaps a zone of elevated atmospheric humidity extends for over 100 m above the stream channel, enabling epiphytic cyanolichens to flourish in the more humid microclimates of the riparian forest canopy compared with drier upland conditions. A similar but less pronounced effect on cyanolichen biomass occurs with elevation: lower elevation forests support a larger cyanolichen biomass than do higher elevation forests even if their proximity to a stream is the same (Howe 1978, Figure 3). The effects of streams on canopy microclimate may be less pronounced at higher elevations

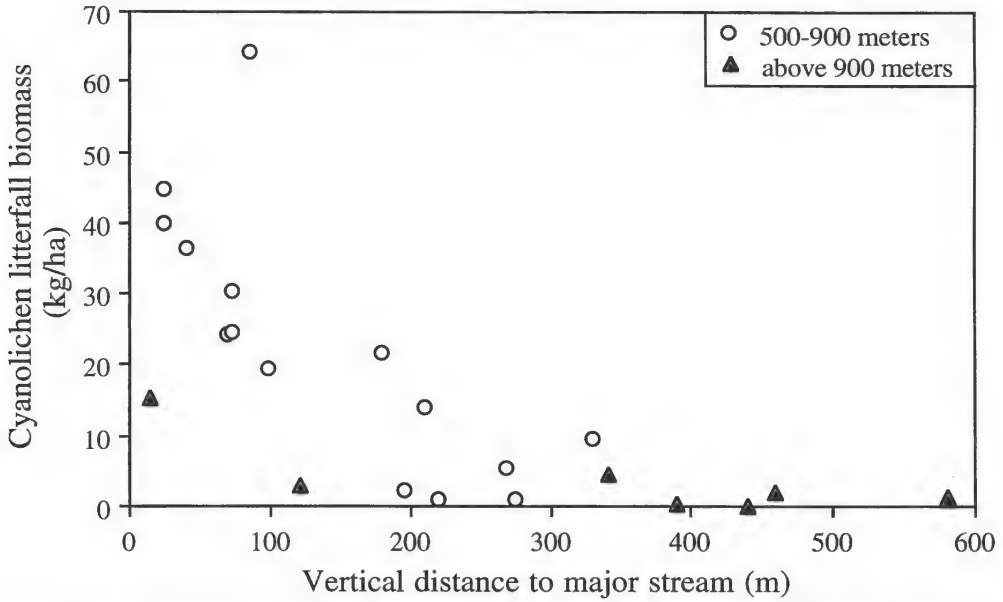

Figure 3. The relationship between epiphytic cyanolichen biomass and proximity to major streams for 22 stands of old-growth Douglas-fir forest in the H.J. Andrews Experimental Forest in the western Oregon Cascades. Open circles represent stands below 900 m elevation. Shaded triangles represent stands above 900 m in elevation. Data from Howe (1978).

simply because stream and channel sizes decrease with increasing elevation. Experimental support for both hypotheses, which predict a tight relationship between cyanolichens and moisture availability, is currently lacking.

If epiphytic cyanolichens are restricted to relatively mesic forests, then they should be absent from many inland sites in the Pacific Northwest, including a large portion of westside forests. In fact, epiphytic cyanolichens *are* scarce in forests east of the Cascades in Oregon and Washington. Only the oldest and wettest sites in the interior forests of Idaho and Montana regularly harbor epiphytic cyanolichens (McCune 1984, Lesica et al. 1991). And given the scarcity of cyanolichens in managed forests, nitrogenous inputs from the canopy may currently be significant in only a tiny portion of the current landscape, that is, old-growth forests on lower slopes west of the Cascades. Efforts to bolster cyanolichen biomass in managed forests would benefit from a clearer understanding of the potential of forests to support epiphytic cyanolichens. Such information can easily be obtained by sampling epiphyte litterfall in a large number of forest stands (see below).

Epiphyte Research and Forest Management

Knowledge of epiphyte ecology in the Pacific Northwest is growing rapidly as a result of recent improvements in canopy access techniques and epiphyte sampling methods. The crowns of tall trees can now be safely accessed by ropes in a few hours without the use of harmful bolts or climbing spurs. Such rope techniques are now complemented by permanent installations such as platforms and construction cranes, which give researchers prolonged and intimate contact with the forest canopy. Although direct access to the canopy is essential for detailed studies of epiphyte communities and their arboreal habitat, canopy-based sampling is not always the best approach for larger-scale questions about epiphyte development in forests. These studies require sampling from many stands throughout the landscape. A recently developed litterfall sampling method that permits rapid assessment of epiphyte abundance and diversity at the stand level (McCune 1994) provides a ground-based alternative to more extensive canopy sampling. These alternative approaches are enabling scientists to initiate studies

of epiphytes that will have important implications for forest management.

Maintaining late-successional species in managed forests is one of the most important challenges in forestry. Recent discussions of forest management alternatives in the Pacific Northwest (*e.g.*, Spies et al. 1991) have focused on the retention of living trees and woody debris in harvest units. If propagule dispersal limits epiphyte colonization, epiphyte populations on retained trees could serve as propagule sources for the re-establishment of these species in the regenerating forest canopy. On the other hand, if microclimates or substrates strongly limit rates of propagule establishment, green tree retention would do little to facilitate epiphyte recovery in managed forests. Controlled experiments involving inoculations and transplantations of substrates in tree crowns are needed to resolve this dilemna. Furthermore, the extent to which late-successional epiphyte species can withstand the microclimatic changes following logging is currently unknown, although some of these species are capable of adjusting to the new microclimate in partially exposed trees (Sillett 1994, 1996).

The potential of uneven-aged management to facilitate recovery of epiphytes in managed forests can be explored in two ways. First, we might retrospectively study natural stands whose structure presumably resembles the intended outcome of a modern silvicultural treatment at rotation age. The effects of retained trees on epiphyte distributions in these stands can be determined by both litterfall and canopy sampling (e.g., Peck and McCune, in prep., Sillett 1995a). Second, survival of epiphytes after silvicultural as well as natural disturbances should be monitored from within the canopy.

Viability ratings for epiphytes in the FEMAT report (FEMAT 1993) suggest that persistence of many epiphyte species will require creation of old-growth characteristics in managed stands. Existing data are insufficient to evaluate the capacity of westside forests to support epiphytes, however, given the high spatial and temporal variability in epiphyte distributions. We recommend an epiphyte litterfall survey of unmanaged stands throughout the Pacific Northwest. These data could be used to develop a model that would help agencies set realistic targets for epiphyte recovery in managed forests.

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Dwarf Mistletoes in Forest Canopies

Abstract

Dwarf mistletoes (*Arceuthobium* spp.) are parasitic flowering plants found throughout much of western North America on members of the Pinaceae. Heavy infection by these parasites affects biomass distribution on individual trees, and hence within forest canopies. Most dwarf mistletoes induce the formation of witches' brooms on infected hosts, and these brooms can significantly alter the structure of forest canopies as well. Conversely, forest canopy structure greatly affects horizontal and vertical spread of dwarf mistletoes. Dwarf mistletoes interact with other organisms that also inhabit forest canopies, such as birds, mammals, insects, and fungi. The principal interaction is the mistletoes serving as a food source for these organisms, but birds and mammals also use witches' brooms as nesting and foraging sites. Another interaction is long-range dissemination of dwarf mistletoe seeds by animal vectors, primarily birds and squirrels.

Introduction

Dwarf mistletoes (*Arceuthobium* spp., Viscaceae) are parasitic flowering plants that parasitize members of the Pinaceae in North America, Central America, Asia, and Africa. Because dwarf mistletoes are widespread in the western United States and Canada and most of the commercially important conifers of this region are severely parasitized by one or more dwarf mistletoes, foresters consider the dwarf mistletoes to be serious forest pests (Hawksworth and Wiens 1972, 1995). Heavily infected trees die prematurely, have reduced growth in height and diameter, and are often predisposed to attack by other diseases and insects (Hawksworth and Wiens 1972, 1995). Therefore, resource managers in many private, state and federal land management agencies have implemented strategies specifically designed to reduce the damage caused by dwarf mistletoes. Despite these efforts, dwarf mistletoes are common inhabitants of canopies in western forests.

My discussion of the dwarf mistletoes as components of forest canopies will concentrate on dwarf mistletoe population dynamics, witches' broom formation, effects of dwarf mistletoes on forest canopy structure and what we know about the ecological interactions between dwarf mistletoes and other forest canopy inhabitants.

Population Dynamics

To understand how dwarf mistletoes function in and affect forest canopies, how these parasites spread and intensify within forests (population dynamics) must first be examined. This examination will include a short discussion of the life cycle and seed dispersal mechanism. Hawksworth and Wiens (1995) provide a more detailed discussion of these processes.

The dwarf mistletoes are dioecious seed plants that have an unusual method of seed dissemination. Fruits produced on female plants mature in the late summer to early winter, contain one seed per fruit, and discharge the seed explosively (Hinds et al. 1963). Seeds are expelled at an initial velocity of about 27 m/sec and can fly as far as 15 m, depending on several factors (Hinds and Hawksworth 1965, Hawksworth and Wiens 1972, 1995). Seeds are coated with a substance called viscin that acts like a glue and allows dispersed seeds to adhere to objects they strike.

Seeds that land on susceptible trees can initiate new infections. Thousands of seeds are dispersed from heavily infected trees, but only about 5 percent of the dispersed seeds are estimated to land on a potential host and only 1-2 percent of those seeds establish successful infections (Hawksworth and Wiens 1972, 1995).

About two years after infection occurs, mistletoe shoots appear on the outside of the branch. In another two years, shoots produce flowers, and pollination occurs. In another 5-19 months, mature fruits disperse their seeds. On the average, the entire life cycle takes about 4-7 years to complete, depending on the species of dwarf mistletoe.

Because dwarf mistletoes are primarily disseminated by the explosive seed dispersal mechanism, forest canopy structure and density greatly influence spread of these parasites. Rates of ver-

tical spread in individual trees is largely governed by crown characteristics. Species with open crowns, such as pines (*Pinus* spp.), permit more rapid vertical spread. Species with dense crowns, such as true firs (*Abies* spp.), have less rapid vertical spread because their dense crowns influence seed flight more than trees with open crowns (Hawksworth 1965, 1969, Scharpf and Parmeter 1976, 1982). In addition, crown structure influences horizontal spread from tree to tree. Canopies composed of tree species with open crowns may allow more seeds to escape from within crowns and thereby provide less screening to prevent infection of nearby crowns. This factor probably has less influence on horizontal spread than on spread of dwarf mistletoes within individual trees, however (Parmeter 1978).

Tree density, which directly influences the canopy structure of a forest, also influences dwarf mistletoe population dynamics. Generally, dwarf mistletoes spread more rapidly in open canopy structures (lower densities of trees) than in dense canopy structures (Parmeter 1978). In areas with few trees, canopies may be so far apart that mistletoe seeds cannot reach neighboring canopies. Beyond some critical distance that varies with canopy height, topography, and the species of dwarf mistletoe, the probability of seed dispersal from one tree to another is unlikely. As distance between tree crowns decreases between infected and healthy trees, the probability of seeds reaching other trees increases. When canopies close, they screen seeds from reaching beyond the trees immediately surrounding infected trees. In addition, spread is influenced by the number of unsusceptible trees with crowns intermixed between those of susceptible trees (Parmeter 1978, Geils and Mathiasen 1990).

Probably the most clearly understood concept in dwarf mistletoe population dynamics is the effect of canopy height structure. In dwarf mistletoe-infested forests with different crown heights, the crowns of small trees are constantly exposed to dwarf mistletoe seeds from above. In these forests, the crowns of susceptible smaller trees can rarely remain free of increasing dwarf mistletoe populations. That the horizontal and vertical spread of dwarf mistletoes is more rapid in forests with multistoried canopies than in forests with single-storied canopies is well documented (Gill and Hawksworth 1954, Kuijt 1955, Kimmey and Graham 1960, Hawksworth 1961, Scharpf and Hawksworth 1968, Scharpf and Parmeter 1976, 1982, Parmeter and Scharpf 1989, Geils and Mathiasen 1990).

Dwarf mistletoe population dynamics is greatly influenced by management activities because they obviously influence stand density, species composition and forest canopy structure. In some forests, dwarf mistletoe infection is undoubtedly greater because past forestry practices, such as high grading or partial cutting, have left forests more open, created multistoried canopies, or removed healthy or unsusceptible trees and left infected trees. These practices have often greatly favored population increases of dwarf mistletoes in forest canopies (Parmeter 1978, Maffei and Beatty 1988).

Along with past logging practices, the avid suppression of wildfire for the past 80 years has affected dwarf mistletoe populations. Fire is the primary natural disturbance that has influenced dwarf mistletoe population distribution in large forested areas (Alexander and Hawksworth 1975, Wicker and Leaphart 1976). Where large areas have been destroyed by intense wildfire, the replacement forests are free of dwarf mistletoes except at their margins. Because dwarf mistletoes slowly reinvade these forests at an average rate of only 30-60 cm/year (Hawksworth 1958, 1960, 1961, Shea and Stewart 1972, Wagener 1965, Crane and Fischer 1986), these replacement forests can remain free of dwarf mistletoes for many years. Because of patchy fuel accumulations and topographic features such as rock outcrops, even large, intense fires frequently leave individual or groups of infected trees within fire boundaries. These trees serve as sources of new infection as new regeneration becomes established after the fire. Frequently, dwarf mistletoe populations are centered around old, infected residuals that have survived fires and serve to reinfect the replacement trees in their immediate vicinity (Shea and Stewart 1972). This reinfection is certainly common in the dwarf mistletoe-infested stands of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western larch (*Larix occidentalis* Nutt.) stands throughout much of the Pacific Northwest (Alexander and Hawksworth 1975, Wicker and Leaphart 1976, Crane and Fischer 1986).

Heinselman (1970) contends that because of the fire exclusion policy of public and private forestry protection agencies and organizations,

dwarf mistletoe populations in forested areas have greatly increased. Fire exclusion has helped create multistoried canopies which are conducive to increasing dwarf mistletoe populations and have essentially eliminated this natural control mechanism for dwarf mistletoes in unmanaged forests.

Witches' Brooms

One of the principal effects dwarf mistletoes have on their hosts, and hence on the canopies of infested forests, is that they induce the formation of witches' brooms (Figure 1). Witches' brooms exhibit several characteristics atypical of healthy host tissue, such as increased longevity (Weir 1916), elimination or reduction of cone and seed production by broomed branches (Bonga 1964, Kuijt 1969), increased branch elongation on some host species (Hawksworth 1961, Tinnin and Knutson 1980), increased biomass relative to healthy branches of the same age (Tinnin and Knutson 1980), or decreased number, length, and mass of needles (Broshot et al. 1986.). A given species of dwarf mistletoe tends to stimulate brooms of a similar type on each infected principal host and on closely related alternate hosts (Hawksworth and Wiens 1972, Tinnin et al. 1982).

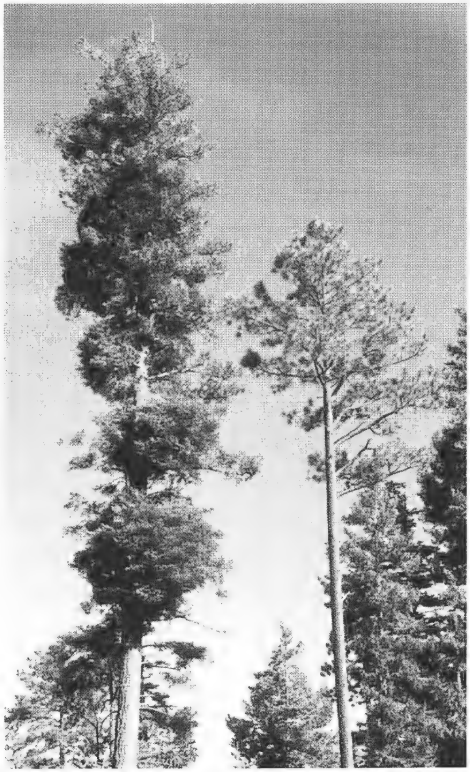

Figure 1. Witches' brooms caused by dwarf mistletoe infection on Douglas-fir in east-central Washington.

Witches' brooms have been characterized based on the pattern of infection, within the infected branches of the brooms, by their general shape, or their growth habit (Kuijt 1955, 1960, Hawksworth 1961, Hawksworth and Wiens 1972, 1995, Tinnin and Knutson 1980, Tinnin et al. 1982).

Formation of witches' brooms as a response to infection by dwarf mistletoes is thought to be related to an imbalance in one or more plant growth regulators in infected host tissue. Paquet (1979) and Schaffer et al. (1983) detected increased concentrations of cytokinins in infected branches compared to healthy branches of the same age. Livingston et al. (1984) reported increases in cytokinin and indole acetic acid concentrations and decreases in abscisic acid, in dwarf mistletoe-infected host tissue of black spruce (*Picea mariana* (Mill.) B.S.P.). The exact mechanisms through which these substances are related to witches' brooms remain unclear. Whether increased concentrations of cytokinins, indole acetic acid, or both disrupt the dominance exerted by the apical meristem of infected branches, thereby allowing the rapid growth of lateral twigs, or whether decreased concentrations of abscisic acid cause this phenomenon, is uncertain. How dwarf mistletoes cause changes in plant growth regulator concentrations is also not understood. Does the parasite produce and then release these substances into the host tissue to cause concentration increases? Or does it stimulate the host to produce additional amounts (or, for abscisic acid, reduced amounts) of the substances? Some evidence suggests that the first mechanism may be responsible for the increases in plant growth regulator concentrations (Paquet 1979, Schaffer et al. 1983), but more research is needed on this topic. A few dwarf mistletoes do not induce witches' brooms (Hawksworth and Wiens 1972, 1995), but again it is unclear why.

Dwarf mistletoe parasitism greatly alters the host's carbon allocation. Obviously, because the parasite is absorbing nutrients from its host, these nutrients are no longer available to the host. Eventually, the host begins to suffer as the dwarf mistletoe population it is supporting reaches a level where

the host cannot provide enough nutrients to supply the parasite's needs as well as its own. Gradually, host growth in height and diameter begins to decrease. Trees weakened extensively by dwarf mistletoe parasitism may be attacked by other diseases and insects that contribute to eventual death. As heavily infected trees die, their crowns thin and needles become chlorotic. Uninfected branches and witches' brooms in the upper crown often die first. Frequently, dead tops develop on these trees (Knutson 1983). The last branches to fade and die are typically the largest brooms near the bottom of the crown. This process usually takes several years, depending on the age of the tree and a variety of environmental factors. Witches' brooms are believed to act as nutrient sinks and command a large share of the metabolites produced by the host (Hull and Leonard 1964a, 1964b, Leonard and Hull 1965, Clark and Bonga 1970, Miller and Tocher 1975, Knutson 1983). Little information is available on the actual energy demands of infected branches compared to healthy branches, however. Careful measurements of the energy budget of infected trees and the effects of dwarf mistletoe parasitism on carbon allocation within infected branches are needed (Wanner and Tinnin 1986).

Changes in Canopy Structure Related to Dwarf Mistletoe Infection

Forests infested with dwarf mistletoes have very different canopy structures than do similar noninfested forests, for several reasons. As infection spreads and intensifies, the crown structure of trees changes dramatically. As more branches become infected, more brooms form, until a tree may become one large mass of dwarf mistletoe brooms (Figure 2). As dwarf mistletoe infection spreads through a forest, the whole canopy structure becomes dominated by trees with large witches' brooms, trees with spike tops, and dead trees with old brooms that may remain on trees for several years (Figure 3). These changes in canopy structure take many years.

Often, dwarf mistletoe infection is patchy within a stand, with discrete infection centers. Over time, many of these centers may coalesce to form infestations that cover many hectares. These forests consist of a mixture of dead trees, heavily broomed older trees, lightly infected younger trees, and some trees that have escaped infection for various reasons. As trees die, directly or indirectly

Figure 2. Western larch infected with dwarf mistletoe in northern Idaho. Tree on right is heavily infected and tree on the left is moderately infected. Note the difference in crown structure between the two trees.

as a result of parasitism by dwarf mistletoe, many snags are created within infested stands. Eventually, gaps develop in the forest canopy. These processes alter the canopy structure of the infested stand to the point where it no longer resembles the canopy structure of a similar, but uninfested stand. In mixed species forests, where one or more less susceptible or immune species are intermixed among highly susceptible species, the effect of dwarf mistletoe infection on canopy structure will be less pronounced.

Given that many other organisms directly benefit by using dwarf mistletoes for food or witches' brooms for shelter, or indirectly by using dead trees for nesting sites as do many cavity-nesting animals, the benefits to wildlife habitat derived from this gradual canopy structure conversion

Figure 3. Lodgepole pine stand heavily infested with dwarf mistletoe in northern Colorado. Canopy is composed of broomed and dead trees. Most of the understory trees are infected but are not yet heavily broomed.

could be substantial (Tinnin et al. 1982, Tinnin 1984). The infested stand is as highly complex ecologically (if not more so) as an uninfested stand and is ecologically distinct in its function and canopy structure. However, there are few studies comparing species diversity of dwarf mistletoe-free forests with similar, infested forests. Only in recent years have investigators examined these relations (Tinnin et al. 1982, Tinnin 1984, Bennetts et al. 1991, Sever et al. 1991).

Dwarf Mistletoes and Other Forest Canopy Inhabitants

Complex interrelations exist between dwarf mistletoes and a wide variety of other organisms that inhabit forest canopies in western North America (Hawksworth and Wiens 1995). Insects pollinate dwarf mistletoes and mistletoe shoots, pollen and nectar serve as food for various fungi, arthropods, birds, and rodents and other mammals. Animals forage among mistletoe shoots and witches' brooms. Witches' brooms serve as nesting sites for several species, and animals can serve as seed vectors for dwarf mistletoes. These various interactions will be discussed separately below.

Arthropods and Dwarf Mistletoes

Dwarf mistletoes harbor numerous arthropods, but we know little about the ecological relations among them. Insects are thought to play an important role in pollinating dwarf mistletoes (Hawksworth 1961, Stevens and Hawksworth 1970, 1984, Gregor et al. 1974, Penfield et al. 1976, Player 1979, Hawksworth and Wiens 1995). The principal pollinators identified thus far are thrips (Thysanoptera), ants (Hymenoptera), and a wide variety of flies (Diptera).

Several species of arthropods, especially Lepidoptera larvae, feed on dwarf mistletoe shoots, and some are thought to be specific to dwarf mistletoes (Stevens and Hawksworth 1970, 1984, Hawksworth and Wiens 1995). Feeding by insects is sometimes highly destructive to the shoots (Scharpf and Koerber 1986), but little is known about the effects of insect feeding on dwarf mistletoe populations over long periods. Only a few

insects that feed on dwarf mistletoes have been commonly collected or have had their life histories studied (Stevens and Hawksworth 1970, 1984, Hawksworth and Wiens 1995). These include the following Lepidoptera: *Filatima natalis* (Heinrich), *Dasypyga alternosquamella* Raganot, and *Mitoura spinetorum* (Hewitson). Each of these insects is specific to dwarf mistletoes and has been destructive to shoots in some locations (Heinrich 1921, Hawksworth 1961, Shields 1965, Stevens and Hawksworth 1970, 1984). Another species, *Mitoura johnsonii* Skinner, occurs on hemlock dwarf mistletoe from Oregon to British Columbia (McCorkle 1962).

Another group of arthropods commonly found associated with dwarf mistletoe shoots is plant bugs in the genus *Neoborella*, particularly *N. tumida* Knight. This species is a widespread associate of several dwarf mistletoes throughout the western United States (Stevens and Hawksworth 1970, 1984, Hawksworth and Wiens 1995). Although plant bugs are commonly associated with dwarf mistletoe shoots, they seem to cause little if any observable damage to the shoots.

One of the most interesting and easily observed arthropods found frequently associated with dwarf mistletoes, particularly in the Southwest, is a spittlebug, currently classified as *Clastoptera distincta* Doering (Stevens and Hawksworth 1984, Hawksworth and Wiens 1995). Spittlebugs are sucking insects, some of which are important plant pests. Their common name describes their nymphs, which live and feed in masses of a secreted material that resembles spittle. High populations of this insect have destroyed large numbers of dwarf mistletoe shoots (Hawksworth 1961), but spittlebug populations are seldom large enough to seriously affect dwarf mistletoe populations over large areas.

Several species of mites have been found associated with dwarf mistletoes. The life histories, habits, and ecological relations of dwarf mistletoe-inhabiting mites have received little study, however (Stevens and Hawksworth 1970, 1984, Hawksworth and Wiens 1995).

Spiders have been found associated with dwarf mistletoes in Colorado (Jennings et al. 1989). More than 20 spider species were found to be associated with three different species of dwarf mistletoe. The ecological relationships of these spiders with dwarf mistletoes have not been investigated in any detail. Possible relations include spiders as pollen vectors or deterrents to pollen dispersal (webs catch pollen), as predators of insects that are directly associated with dwarf mistletoes (pollinators or herbivores), and as predators of casual insect visitors to dwarf mistletoes (Jennings et al. 1989).

Because tree mortality greatly affects the stand and canopy structure of western forests, insects that kill trees and their relations with dwarf mistletoes must be mentioned. Much of this information is based on observations, but some quantitative data are available. Most of the completed work has dealt with the relations between dwarf mistletoes and bark beetles in the genus *Dendroctonus*. Dwarf mistletoes evidently do increase the susceptibility of infected trees to attack by certain bark beetles. The best documented examples are for western pine beetle (*Dendroctonus brevicomis* Lec.) and mountain pine beetle (*D. ponderosae* Hopkins) in ponderosa pine (*Pinus ponderosa* Laws.)(Stevens and Hawksworth 1984). In addition, "secondary" insects (*Ips* spp. and *Melanophila* spp.) have often been reported to attack and kill dwarf mistletoe-infected trees. Stevens and Hawksworth (1984) and Hawksworth and Wiens (1995) present excellent summaries of the reported relations between tree mortality, insects, and dwarf mistletoes.

Fungi and Dwarf Mistletoes

Several species of fungi have been identified as hyperparasites of dwarf mistletoe shoots (Kuijt 1963, Wicker and Shaw 1968, Hawksworth et al. 1977, Scharpf 1986, Hawksworth and Wiens 1995). Table 1 lists these fungi and their known geographic distribution in western North America.

Several species of fungi infect branch tissue that is already infected by dwarf mistletoes. These fungi are referred to as "canker fungi" because they kill the cambium of the host branch as well as the dwarf mistletoe. Most of these fungi have been described in association with the western hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G.N. Jones subsp. *tsugense*) in British Columbia (Baranyay 1966, Funk and Baranyay 1973, Funk 1981, Funk and Smith 1981). Little is known about how these fungi affect dwarf mistletoe populations. One of these fungi, *Nectria macrospora* (Wr.) Ouellette, has been reported to reduce dwarf mistletoe reproduction in some areas (Funk et al. 1973, Smith and Funk 1980).

TABLE 1. Fungi known to be hyperparasites of dwarf mistletoe shoots in western North America and their known geographical distribution based on parasitism of dwarf mistletoes.[1]

Fungus	Reported Distribution
Wallrothiella arceuthobii (Peck) Sacc.	United States, Canada, and Mexico
Colletotrichum gloeosporioides Penz.	Western United States, Canada, and Mexico
Cylindrocarpon gillii (Ellis) J. A. Muir	Western United States, Canada, and Mexico
Cylindrocarpon sp.	Southern Mexico
Alternaria alternata (Fr.) Keissler	Manitoba, Canada
Metasphaeria wheeleri Linder	California
Herpotrichia juniperi (Duby) Petrak	California
Pestalotia maculiformans Guba & Zeller	Washington
Pestalotia heterocornis Guba	Dominican Republic

[1] Based on information in: Kuijt 1963; Hawksworth et al. 1977; Scharpf 1986; Hawksworth and Wiens 1995.

Scharpf (1969, 1983) demonstrated that *Cytospora abietis* Fr. is consistently associated with dwarf mistletoe infections of red fir (*Abies magnifica* A. Murr.) and white fir (*A. concolor* (Gord. & Glend.) Lindl.) in California. About 20 percent of the dwarf mistletoe-infected branches he examined were also infected by *C. abietis*. Scharpf concluded that infection by this fungus is responsible for a reducing the total dwarf mistletoe population on dwarf mistletoe-infected true firs in California. Filip et al. (1979) reported that *C. abietis* also infected dwarf mistletoe-infected branches on noble fir (*A. procera* Rehd.) and Pacific silver fir (*A. amabilis* (Dougl.) Forbes) in Oregon. They also reported two additional fungi associated with dwarf mistletoe infections on these two true firs: *Cryptosporium pinicola* Linder and *Cylindrocarpon cylindroides* Wollen (the imperfect stage of *Nectria fuckeliana* Booth). Byler and Cobb (1972) reported *N. fuckeliana* infections associated with dwarf mistletoes on bishop pine (*Pinus muricata* D. Don) and white fir in California. Diplodia tip blight (*Sphaeropsis sapinea* (Fr.) Dyko & Sutton) has been associated with dwarf mistletoe infections on both digger pine (*Pinus sabiniana* Dougl.) and bishop pine (Hunt 1969).

A rust fungus, *Peridermium bethelii* Hedgcock and Long, is consistently associated with infections of lodgepole pine dwarf mistletoe (*Arceuthobium americanum* Nutt. ex Engelm.) on lodgepole pine (*Pinus contorta* Dougl. ex Loud.) in the Rocky Mountains and California (Hawksworth et al. 1983). The role of the dwarf mistletoe in the life cycle of the rust is not well understood, however. More work is needed on the relation of the rust and the mistletoe as well as the taxonomic status of the rust (Hawksworth et al. 1983).

Animals and Dwarf Mistletoes

The majority of the investigations on the relations between animals and dwarf mistletoes have been related to animals acting as vectors for long-range dissemination of dwarf mistletoe seeds (Hawksworth and Wiens 1995). This relation has now been well documented by several investigators (Nicholls et al. 1984, 1989, Punter and Gilbert 1989, Hawksworth and Wiens 1995). Although the importance of animal dissemination of dwarf mistletoe seeds remains uncertain, it is undoubtedly responsible for establishing new infection centers at much greater distances than could be attained by the explosive seed dispersal mechanism (Hawksworth and Wiens 1995). Several animals, primarily birds and squirrels, have been identified as vectors of dwarf mistletoe seeds (Table 2).

Another relation that has been well documented between animals and dwarf mistletoes is the use of witches' brooms as nest sites (Table 3) (Hawksworth and Wiens 1995). Whether animals rely on or preferentially select dwarf mistletoe-induced witches' brooms as nest sites is still under study. Recent studies of the northern spotted owl (*Strix occidentalis caurina*) in the eastern Cascade Range of Washington indicate that these owls frequently nest in dwarf mistletoe brooms (Irwin et al. 1989, Richards 1989, Forsman et al. 1990, Martin et al. 1992). Recent observations in

TABLE 2. Animals identified as vectors of dwarf mistletoe seed.[1]

Birds	Mammals
Steller's jay	Red squirrel
Gray jay	Flying squirrel
Three-toed woodpecker	Golden-mantled squirrel
Williamson's sapsucker	American marten
Robin	Least chipmunk
Dark-eyed junco	
Gray-head junco	
Hermit thrush	
Northern saw-whet owl	
Audubon's warbler	
Yellow warbler	
Palm warbler	
Yellow-rumped warbler	
Mountain chickadee	
Cassin's finch	
Pygmy nuthatch	
Chipping sparrow	
Townsend's solitaire	
Red crossbill	
Brown creeper	
Swainson's thrush	
Red-breasted nuthatch	

[1]Based on information in: Nicholls et al. 1984, 1987, 1989; Punter and Gilbert 1989; Hawksworth and Wiens 1995.

western Oregon have confirmed that marbled murrelets (*Brachyramphus marmoratus*) use witches' brooms caused by western hemlock dwarf mistletoe in western hemlock as nest sites (Clint Smith, Oregon Department of Forestry, Salem, pers. comm.). Red, Abert, and flying squirrels also use dwarf mistletoe brooms for nest sites (Farentinos 1972, Hawksworth and Wiens 1995).

Several animals feed on dwarf mistletoe shoots or indirectly on the endophytic system, by chewing and eating dwarf mistletoe-infected bark (Hawksworth and Wiens 1995). Table 4 lists the animals reported to use dwarf mistletoes as a food source. Although the use of dwarf mistletoes as food by various animals is well documented, the importance of dwarf mistletoes in the diet of these animals is uncertain. Much of the use of dwarf mistletoes appears to be during the winter when other food sources are less common or completely unavailable. Dependence by birds, rodents or

TABLE 3. Animals that use dwarf mistletoe-caused witches' brooms for nesting.

Birds	Mammals
Pine siskin	Red squirrel
Gray jay	Abert squirrel
Red crossbill	American marten
Robin	
Raven	
House wren	
Mourning dove	
Western tanager	
Chipping sparrow	
Hermit thrush	
Cassin's finch	
Marbled murrelet	
Northern spotted owl	
Mexican spotted owl	
Great gray owl	
Great horned owl	
Long-eared owl	
Cooper's hawk	
Goshawk	
Sharp-shinned hawk	

[1]Based on information in: Farentinos 1972; Tinnin et al. 1982; Smith, pers. comm. 1994; Hawksworth and Wiens 1995.

TABLE 4. Animals that use dwarf mistletoes as food.[1]

Birds	Mammals
Black-headed grosbeak	Chipmunks
Evening grosbeak	Porcupine
Blue grouse	Elk
Spruce grouse	Mule deer
Richardson grouse	White-tail deer
Ruffed grouse	Red squirrel
Black-capped chickadee	Abert squirrel
House sparrow	
Thrush	
Western bluebird	
Mountain bluebird	
Phainopepla	
Mourning dove	
Robin	
Band-tailed pigeon	

[1]Based on information in: Pinkowski 1981; Tinnin et al. 1982; Crawford et al. 1986; Pederson et al. 1987; Allred 1989; Hawksworth and Wiens 1995.

mammals on dwarf mistletoes has not been reported. Investigators have demonstrated that dwarf mistletoe shoots are highly digestible; they are high in carbohydrates but low in mineral and protein content (Urness 1969, Craighead et al. 1973).

Little information is available on the use of dwarf mistletoe brooms by animals for hiding cover, resting sites, or foraging sites. Martinka (1972) reported the use of brooms for hiding cover by blue grouse (*Dendragapus obscurus*) in Montana. Martens (*Martes americana*) have been observed using dwarf mistletoe-caused witches' brooms for resting sites (Campbell 1979, Hauptman 1979, Burnett 1981, Spencer 1987, Buskirk et al. 1987). Other animals probably use dwarf mistletoe brooms for cover, resting sites, and foraging sites but these relations are poorly documented.

In general, the relations between dwarf mistletoes and the myriad of organisms that inhabit forest canopies are not well understood. Because dwarf mistletoes are common parasites in western forests, investigators working on forest canopy research should consider the effects of dwarf mistletoes on canopy structure and possible interactions between dwarf mistletoes and other species. We may find that species diversity is much greater within dwarf mistletoe-infested canopies than in the canopies of mistletoe-free forests in the Pacific Northwest, if we examined these canopies more thoroughly. For example, studies in the Front Range of Colorado have demonstrated that the abundance and number of species of passerine birds and the abundance of cavity-nesting birds is higher in dwarf mistletoe-infested ponderosa pine stands than in non-infested stands (Bennetts et al. 1991, Sever et al. 1991). Bennetts et al. (1991) also reported that elk and deer activity were higher in dwarf mistletoe-infested stands. Further studies of this nature may demonstrate that similar relations exist between many other organisms and dwarf mistletoes.

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Interactions of Northwest Forest Canopies and Arboreal Mammals

Abstract

The interactions among Northwest forest canopies and the mammals that inhabit them have been poorly studied. My purpose was to identify interactions among arboreal mammals and canopies that have implications for managers seeking to conserve biodiversity in the Pacific Northwest. I constructed a comprehensive, but parsimonious list of canopy attributes that could be biologically important. I compiled a list of mammals that routinely enter the canopy and ranked them relative to arboreality. I identified which attributes might be important to each species and how the attributes might contribute to maintaining arboreal rodent communities. Forest canopies have 26 categories of attributes of 5 major types: context, seral stage, community type, canopy dimensions, and tree species character. At least 12 species of mammals (excluding bats) use forest canopies, but only 7 should be considered truly arboreal. All but one of the arboreal rodents are limited zoogeographically, or in local distribution, because of needs for specific habitat elements. Only one species, the red tree vole, is totally arboreal; thus, the composition and structure of the arboreal rodent community is conditioned by both canopy and noncanopy features of the forest. Of the canopy attributes, diversity of tree species and abundance of nontree organisms, including lichens, mosses, and rot-inducing fungi, seem especially important to arboreal rodents. Diversity of tree species provides a variety of food (foliage, seed, fruit, nuts, and truffles and mushrooms of fungi symbiotic with the trees). Rot-inducing (and pathogenic) fungi provide cavities for leaf-lichen-moss nests and platforms for lichen-moss-twig nests. Lichens also serve as food.

Introduction

Forest canopies are less accessible to the biologist than is the forest floor and, thus, have been studied less than lower structures. Nevertheless, canopies are rich in life (Denison 1973, Pike et al. 1977, Schowalter 1989) and, around the world, commonly used by a variety of mammals other than human beings, including marsupials, bats, rodents, carnivores, and primates (Nowak 1991). Old-growth canopies in the Pacific Northwest are especially tall (50-90 m) and complex, with multilayered vegetation and diverse structures (Franklin and Spies 1991). This complexity of canopy structure and composition suggests that an in-depth understanding of canopy function will be necessary to ensure that efforts to conserve biodiversity in the Pacific Northwest will be successful. Of course, canopies are not independent of the forest ecosystem; their use and function depend on their biogeographic and synecologic context.

My goal in this paper is to identify interactions among arboreal mammals and canopies in the Pacific Northwest that have implications for the conservation of biodiversity. First, I constructed a comprehensive, but parsimonious list of biologically important canopy attributes. Next, I compiled a list of mammals (excluding bats; see Wunder and Carey this issue) that routinely enter the canopy and ranked them according to the degree to which they use canopies (i.e., arboreality), following the method of Carey (1991). Then, I identified which attributes might be important to each species and how the attributes might contribute to maintaining arboreal rodent communities. Finally, I discuss implications for management and for research.

Canopy Attributes of Biological Importance

All attributes of canopies could have biological importance. Because the attributes are numerous and varied, I constructed a hierarchical classification of canopy attributes (Table 1). The hierarchy begins with spatial and temporal scales, including geographic, geomorphic, and landscape location and stage of forest development and age of tree. Where a canopy is found determines the mix of species that can occur in, or use, the canopy (see Table 2 for mammals). The stage in the development of a community also determines the array of species that can potentially inhabit the canopy. The process of forest development is one of accumulation and redistribution of biomass (Bormann and Likens 1979, Oliver and Larson 1990) among living trees, standing dead trees,

TABLE 1. Attributes of forest canopies of potential biological importance in the Pacific Northwest.

I. Context
  A. Biogeographic Region
    1. Species Available: plants, animals, and their commoness and rarity
    2. General Climatic Regime: effects on species and processes
  B. Geomorphic Location
    1. Species Abundance Patterns: forest, habitat, and community types
    2. Climatic-Disturbance Regimes: phenology, limiting factors, perturbations
    3. Special Habitat Elements: cliffs, caves, talus, wetlands, rivers, etc.
  C. Landscape Context
    1. Composition: community types and ecotones
    2. Heterogeneity: seral stages, interiors, and edges
    3. Grain: patch size, diversity, contiguity, and frequency
    4. Connectivity and Isolation

II. Seral Stage or Stand Condition
  A. Stand Initiation: low, open canopies
  B. Stem Exclusion: dense canopies, sometimes thin; small dead trees; lack of diversity
  C. Understory Reinitiation: slightly open canopy, deepening crowns, few snags
  D. Understory Development: open canopy, medium snags, botanical diversity increasing
  E. Old Growth: high canopy texture, multilayered vegetation, high canopy volume, high species diversity, high size diversity, large snags, large gaps, many associates

III. Community Type

A. Species Composition of Canopy Trees
  1. Diversity of Seed Source: abundance, minimum consistency of production, palatability, food value, synchronicity of seed crop failure
  2. Variety in Architecture: shape, branchiness, branch size, branch angle, leaf or needle size, leaf or needle density
  3. Variety in Life Form: conifer, deciduous hardwood, evergreen hardwood

B. Canopy Associates
  1. Epiphytes: mosses, lichens, ferns, mistletoe
  2. Endophytes: diseases and rot fungi (produce cavities, broken tops)
  3. Invertebrates: slugs, snails, spiders, mites, insects (larvae and adults)
  4. Vertebrates: amphibians, reptiles, birds, and mammals
  C. Other Associates
    1. Understory Woody Plants: foliage, fruits, nuts, seeds, insects, mycorrhizae
    2. Understory Forbs, Ferns, Grasses: foliage, fronds, seed
    3. Forest-floor Mosses and Lichens: nest material
    4. Rhizophere Associates: ectomycorrhizal fungi
    5. Soil Organisms and Microorganisms

IV. Canopy Dimensions
  A. Volume
    1. Total Height
    2. Height to Live Crown
    3. Areal Extent
  B. Density
    1. Canopy Closure
    2. Interconnectedness of Tree Crowns
    3. Layering
  C. Heterogeneity
    1. Texture of Canopy Surface (rugose old growth vs. smooth young, even-aged)
    2. Gaps: frequency and size

V. Tree Species Character
  A. Size and Age of Canopy Trees
    1. Branch Size and Shape
    2. Bark Rugosity
    3. Decadence: broken tops and branches; cavities
    4. Biomass of Fruit or Seed
  B. Species-Specific Attributes
    1. Associates: fungi, mosses, lichens
    2. Phenology: bud, leaf, and seed production
    3. Life Form: size, architecture, growth form, shade tolerance, fire resistance
    4. Health and Longevity: root-, butt-, and top-rots; insects; and disease resistance

TABLE 2. Some mammals using forest canopies, the degree to which they use canopies (aboreality, scale of 0-12), and their distribution in the Pacific Northwest.

Species	Arboreality	Geographic Distribution[1]			
		WWA	WOR	EWA	EOR
Red tree vole (*Phenacomys longicaudus*)	12	-	+	-	-
Western gray squirrel (*Sciurus griseus*)	8	+	+	p	p
Northern flying squirrel (*Glaucomys sabrinus*)	7	+	+	+	+
Douglas' squirrel (*Tamiasciurus douglasii*)	7	+	+	-	-
Red squirrel (*Tamiasciurus hudsonicus*)	7	-	-	+	+
Dusky-footed woodrat (*Neotoma fuscipes*)	7	-	+	-	-
Bushy-tailed woodrat (*Neotoma cinerea*)	6	+	+	+	+
Townsend's chipmunk (*Tamias townsendii*)	4	+	+	-	-
Porcupine (*Erethizon dorsatum*)	3	+	+	+	+
Marten (*Martes americana*)	3	+	+	+	+
Fisher (*Martes pennanti*)	3	p	p	p	p
Raccoon (*Procyon lotor*)	2	+	+	+	+
Forest deer mouse (*Peromyscus oreas*)	1	+	-	-	- -

[1] Distribution in western Washington (WWA), western Oregon (WOR), eastern Washington (EWA), and eastern Oregon (EOR) expressed as present (+), present, but rare (p), and absent (-).

fallen trees, litter, soil organic matter, and a variety of life forms including cryptogams, ferns, forbs, shrubs, shade-tolerant understory trees, fungi, invertebrates, and vertebrates. The accumulation of biomass and its apportionment among diverse life forms leads to a complex ecosystem that allows niche diversifications and increased species diversity within the community (Whittaker et al. 1973, Hutchinson 1978). Thus, at subsequent, and lower, levels in the hierarchy, apportionment of biomass, increased species diversity, and cumulative species-specific effects begin to assume importance. Although I believe the outline of attributes is comprehensive, it certainly is not exhaustive. I will illustrate how many of these attributes are important to mammals; some of them (and others) will be important to bats (Wunder and Carey this issue) and birds (Sharpe this issue). But, I expect (and hope) others will amend and refine the list.

Arboreal Mammals

Carey (1991) developed a scale to measure the degree to which mammals inhabit or frequent forest canopies and called the scale "arboreality." Arboreality is evaluated by ranking a species' use of trees (overstory and understory) and shrubs relative to its use of the forest floor for three activities: travel, nesting and denning, and foraging. Ranks range from 0 (no routine use) to 4 (activity confined to trees and shrubs). The three rankings are summed to obtain arboreality, which ranges from 0 to 12. In the Pacific Northwest, the most arboreal mammal is the red tree vole (Table 2), which occurs only in western Oregon and which conducts almost all its activities high in tree canopies (Maser et al. 1981). Indeed, the red tree vole prefers the lower third of the crowns of the largest trees in old-growth forests (Gillesberg and Carey 1991). At the other end of the scale is the forest deer mouse, the most arboreal of the forest-floor mammals, which travels and forages in understory trees and shrubs and whose abundance increases with understory development, but which has not yet been shown to use tree canopies (Carey and Johnson 1995). Mammals that sometimes den in tree cavities and opportunistically forage in trees (marten, fisher, and raccoon; Novak 1991) receive low rankings (2-3). The porcupine, which regularly sleeps in trees, but prefers rock dens (McLean et al. 1993) and which forages for dwarf mistletoe and cambium in trees, but emphasizes intake of herbaceous plants

(Johnson and Carey 1978) also receives a low ranking (3, Table 2). Townsend's chipmunk regularly forages in the understory, sometimes nests in tree cavities, and is only marginally an arboreal mammal (Table 2, Carey 1991). Thus, for the rest of this paper, I will concentrate on interactions between forest canopies and the seven species of mammals that score ≥ 6 points on the 12-point scale.

Interactions Between Arboreal Mammals and Forest Canopies

Red tree vole.—The red tree vole has the narrowest niche of the arboreal mammals. It spends almost all its time in trees (rarely traveling between trees on the ground), eats conifer needles (primarily Douglas-fir, *Pseudotsuga menziesii*, needles), and obtains water from fog drip on needles, moss, and lichens (Maser et al. 1981). Nests of twigs, resin ducts (leftovers from eaten needles), whole needles, and lichens are built on large branches or on whorls of branches. Nests are also excavated in heavy moss layers on large branches, and some nests are in cavities in trees (Gillesberg and Carey 1991). The red tree vole is most abundant in old-growth forests, in large trees, and in areas where crowns interweave (enhancing access to food, facilitating social interactions, and providing numerous escape routes). Limiting factors include crown depth and stability (young tree crowns are constantly moving upward, requiring nest relocation), crown connectedness (contiguity), canopy volume and density, and areal extent and connectivity of mature and older forests. Populations of red tree voles can grow slowly under good conditions; ability to disperse and recolonize vacated habitats is probably low even under favorable conditions (contiguous crowns). The red tree vole seems particularly adapted to the stable conditions of old-growth Douglas-fir (Maser et al. 1981, Carey 1991).

Western gray squirrel.—The western gray squirrel has a broader niche than the red tree vole: it eats conifer seed, oak (*Quercus* spp.) acorns, the seeds, nuts, and fruits of other trees and shrubs, mushrooms, and truffles. It builds its nest of twigs, lichens, and mosses in coniferous trees and will use cavities in coniferous or deciduous trees. Despite its relatively broad niche, it has a narrow habitat in Oregon and Washington, primarily occupying Oregon white oak (*Q. garryana*)-Douglas-fir and Oregon white oak-ponderosa pine (*Pinus ponderosa*) communities < 1 km from water (streams, ponds, wetlands) and of > 2 ha (Ryan and Carey 1995). In the southern parts of its range, the squirrel occupies the wide array of oak communities available there. In Oregon and Washington, it is sometimes found in plantations of nut-bearing trees. The Oregon white oak communities, however, tend to be ecotonal, merging with native prairies, streamside communities, and wetlands, and easily lost to succession in the absence of wildfire. They are often small in area. Connectivity, in the form of coniferous and riparian forests, seems to be important for travel by gray squirrels and colonization of unoccupied oak-conifer woodlands. Within the oak communities, the presence of large conifers for escape cover, nest sites, and food (seed) is mandatory. Interconnectedness of tree crowns for travel and escape is important. The diversity of nut- and seed-bearing trees and shrubs, for example bigleaf maple (*Acer macrophyllum*), Oregon ash (*Fraxinus latifolia*), California hazel (*Corylus cornuta*), and vine maple (*A. circinatum*), is important for providing high-quality food for the squirrels in years of acorn crop failure.

Northern flying squirrel.—The flying squirrel has a relatively narrow niche as a cavity-dwelling mycophagist, but a broad habitat, occupying a range of conifer, deciduous, and mixed-species forest communities and seral stages (Carey 1991). The flying squirrel is most abundant in old-growth Douglas-fir and mixed-conifer forests (Carey et al. 1992, Carey 1995); their abundance is low in northern forests dominated by western hemlock (*Tsuga heterophylla*) or Pacific silver fir (*Abies amabilis*). The difference in abundance may be due, in part, to the northern forests being colder and more subject to snowfall (with concomitant direct stresses on the lightly built squirrel), but it also appears to be related also to differences in diversity of ectomycorrhizal fungi, which are more diverse in old than young forests and in southern than northern forests in the Pacific Northwest. Fruiting bodies (mushrooms and truffles) of ectomycorrhizal fungi are the primary food of northern flying squirrels, although lichens can be important winter foods (Maser et al. 1986, Carey 1991, Carey et al. 1992, Carey 1995). The flying squirrel uses stick nests of other species, stick-moss-lichen nests it constructs itself, and moss-lichen-cambium nests it constructs in natural cavities and cavities created by woodpeckers. Cavity

nests are more predator-proof, more resistant to wind and precipitation, and thermally superior to stick nests (Carey and Sanderson 1981). Cavities arise out of the interaction in living trees of damage, infection by rot-inducing fungi, and time, with the excavation of rotten wood by woodpeckers and other birds in both living and standing dead trees. Most woodpecker-created cavities are in large, old snags (> 80 cm dbh), and thus are most abundant in old-growth forests (Carey et al. 1991). Arboreal lichens and mosses and terrestrial mosses are important nest materials. Flying squirrel abundance is correlated with understory development, particularly ericaceous shrubs (Carey 1995). These shrubs provide cover for squirrels foraging on the ground for truffles, and may enhance mycorrhizae and truffle production by forming symbiotic relations with the mychorrhizae of trees. Understory composition and abundance reflects both soil moisture and canopy openings (Carey et al. 1991); woody understory development is often greatest in the vicinity of large dead trees or in canopy gaps (Carey 1995). The interactions of canopy openings resulting from the death of large trees and the subsequent development of woody understories, the cavities constructed by woodpeckers in large dead trees, and the diversity of canopy and understory woody plants that promotes fungal diversity make old-growth forests, especially southern Oregon old-growth forests, the optimal environment for flying squirrels. Populations are lower in younger forests and the squirrels adapt to these less hospitable environments by constructing nests from dead twigs and branches, using dens in residual trees and deciduous trees, and moving long distances to forage (unpublished data). Because of their ability to use a range of seral stages, flying squirrels become isolated only by very early stages of forest development and nonforested environments; however, populations in patches of old growth can be substantially reduced through predation (Carey et al. 1992).

Douglas' squirrels and red squirrels.—These two congeners are specialists at exploiting conifer seed as food. The Douglas' squirrel is adapted to western hemlock-Douglas-fir forests (lightly constructed cones), the red squirrel, to forests with ponderosa pine and lodgepole pine (*Pinus contorta*) and heavily constructed or serotinous cones (Smith 1970, 1981). Both species respond to seed abundance with immigration, increased reproduction, and increased juvenile survival and to seed scarcity by switching to fungi or a limited array of other seed (California hazel, for example), decreased reproduction, emigration, starvation, and decreased survival. Both species will eat mushrooms and truffles when they are available (Maser et al. 1978). In the spring, Douglas' squirrels are equally abundant among young, mature, and old-growth forests (Carey 1989), but in the winter, when food is most scarce, they are most abundant in old forests (Buchanan et al. 1990). The large, old trees and the diversity of tree and shrub species in old forest provide a more dependable supply of food than the young trees, often of one species, in young forests (Carey 1991). Conifers and *Tamiasciurus* have coevolved: trees undergo synchronous failures in cone crops, which reduces squirrel populations, and the squirrels maintain individual territories, which reduces competition for seed and fungi (through spacing), and store food to eat in times of seed scarcity (Smith 1970). Fallen trees and low dead branches provide perch sites from which the squirrels can search for competitors (and predators) while eating. Streams, seeps, and large fallen trees and the moist soil beneath them provide storage sites for fir and hemlock cones (moisture is necessary to keep the cone from opening and spilling its seed). Both squirrels build stick nests lined with mosses, lichens, or grass and build moss-lichen-grass nests in tree cavities. But these squirrels are larger and more robust than flying squirrels and do not seem as tied to cavities. Food seems to be the limiting factor (Carey 1991).

Dusky-footed woodrat.—This species, native to riparian forests in the California chaparral, reaches its northern limits in Oregon, where it inhabits mixed-evergreen and mixed-conifer forests in the Klamath Mountains and interior river valleys. It is most abundant in riparian forest and has a bimodal distribution in upland forests, being most abundant in stand initiation and early stem exclusion stages, rare in stem exclusion and understory reinitiation stages with little understory, and moderately abundant where understory is developed, including old growth (Carey et al. 1992). The dusky-footed woodrat has adapted numerous aspects of its life history to allow it to feed on evergreen sclerophylls high in fiber, tannins, and related polypeptides that are toxic to many mammals (Atsatt and Ingram 1983). This specialization provides the woodrat with a distinct niche; however, it can avail itself of many other

foods, including fungal fruiting bodies. The woodrat makes its houses of sticks and woody debris both on the ground and in trees. It preferentially travels through the understory rather than on the forest floor, where the rustle of dried leaves reveals its presence to predators. It seems to be most limited by the abundance of evergreen sclerophyllous understory, area of suitable stand condition, and connectivity between suitable patches (Carey 1991).

Bushy-tailed woodrat.—The bushy-tailed woodrat is usually an occupant of rock outcrops and talus slopes in shrub and forest communities. Adequate rock shelter is the most important resource for this woodrat in areas with cold weather and heavy snowfall (Escherich 1981). In the relatively warm, low-elevation, transitional and mixed-conifer forests of southwestern Oregon, it also uses cavities in standing and fallen trees and builds houses of sticks and woody debris in tree hollows, on the ground, and on branches in trees. The bushy-tailed woodrat has a broad diet and, in southwestern Oregon, is abundant in streamside forests and other forests with well-developed understories and tree cavities (Carey 1991). Because of its social system of one territorial male with a harem of two or three females, bushy-tailed woodrats occur in small, scattered populations. Thus, area and connectivity of suitable patches of habitat and predation seem to be limiting factors.

Conclusions

Biogeography seems to be the most important determinant of the diversity and abundance of mammals that use canopies in the Pacific Northwest. The southwestern Oregon transition and mixed-conifer forests are characterized by a diversity of plants, fungi, and mammals and a mild climate. Next, presence of cavities in trees (and the rot that is integral to cavity formation) and the woodpeckers that excavate the cavities are important determinants of abundance of arboreal mammals. Similarly, lichens and mosses in the canopy and on the forest floor are insulating materials and important components of arboreal rodent nests. Tree species diversity and developed understories tend to increase canopy volume, interconnectedness of crowns, and abundance, diversity, and dependability of food sources round out within-stand habitat requirements of the rodents. Volume and extent of the canopy of suitable habitat and connectivity to other patches of suitable habitat also seems important. Other species also benefit from overstory diversity that promotes dependable seed sources (e.g., forest-floor small mammals); cavities for den sites (marten, fisher, raccoon, and many birds); large branches for nesting sites; and canopy openings that promote understory development (e.g., *Strix occidentalis,* Carey et al. 1992).

My review clearly indicates that trees alone do not constitute a forest canopy. Various other organisms associated with trees—including fungi, mosses, lichens and vascular plants in the understory—help determine canopy quality as habitat for arboreal rodents. The presence of arboreal rodents, keystone species, provide a prey base for many vertebrate predators and enhance ecosystem function through fungal spore and seed dissemination (Carey 1991). Research seems especially lacking on the importance of canopy epiphytes and invertebrates (food sources for many mammals and birds) as elements of biodiversity. Management of canopies must be based on knowledge and hypotheses (where data are lacking) about processes, functions, and structure, not on structure alone.

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Use of the Forest Canopy by Bats

Abstract

Of the 15 species of bats in the Pacific Northwest, 11 are known to make regular use of the forest canopy for roosting, foraging, and reproduction. This paper reviews roosting requirements, foraging, and the importance of landscape-scale factors to canopy-using species in the Northwest. Many northwest bats use several different types of tree roosts. Common roosting sites are in cavities, crevices, and foliage. Factors that may be important in roost site selection include microclimate, roost structure, crown architecture, canopy tree age and species, bark characteristics, foliage density, and stand and landscape composition. Some representative Pacific Northwest cavity- and crevice/bark-roosting species include the little brown bat *(Myotis lucifugus)*, silver-haired bat *(Lasionycteris noctivagans)*, and long-legged bat *(M. volans)*. Only two Pacific Northwest species are known to roost in foliage. Several species forage in forest gaps, along forest edges, or in riparian areas. Long-eared (*M. evotis)* and Keen's *(M. keenii)* bats may forage within the forest canopy, although foraging behavior of these species in the Pacific Northwest is not well documented. Stand- and landscape-scale complexity may be important in providing bats with the abundance and diversity of roost, foraging, and hibernation sites they require.

Introduction

Little work has been done on forest canopy use by bats in the temperate region, particularly in the Pacific Northwest. Moreover, the understanding of the significance of the forest canopy to bats is complicated by the fact that few temperate species are restricted to any one habitat type for foraging and roosting. Most species meet only some of their requirements within the forest canopy and must go outside the canopy to satisfy the remainder of their needs. The term canopy is used here in the broadest sense to encompass all components (trunks, as well as branches and foliage) of the upper parts or crowns of trees that make up forest stands. A detailed list of canopy attributes of potential significance to bats and other canopy species may be found in Carey (this issue).

About 11 species of Pacific Northwest bats appear to regularly use the forest canopy. An additional two species are occasional canopy users (the fringed bat, *M. thysanodes* and the western small-footed bat, *M. ciliolabrum*) (Table 1). Forest bat communities in the Pacific Northwest are made up of some six to eight *Myotis* species and four non-*Myotis* species. The most frequently encountered species include the little brown bat *(M. lucifugus)*, the Yuma bat (*M. yumanensis)*, the California bat (*M. californicus)*, the long-legged bat (*M. volans)*, the long-eared bat (*Myotis evotis)*, the big brown bat (*Eptesicus fuscus)*, the silver-haired bat (*Lasionycteris noctivagans)* and the hoary bat (*Lasiurus cinereus)* (Christy and West 1993). Townsend's big-eared bat (*Plecotus townsendii*) also forages in forested environments.

Bats use the canopy for a variety of purposes, including roosting, foraging, and reproduction. In this paper, we will examine the use of the forest canopy by Northwest bats for roosting and foraging. The importance of landscape composition to bats, will also be discussed.

Roosting

The roosting ecology of bats has been reviewed by Kunz (1982a). Species diversity and population size of colonial bats appear to increase with increased roost availability and diversity (Humphrey 1975, Findley 1993). Areas that offer a variety of tree, cliff, and cave roosts, often support the largest number of bat species and individuals (Humphrey 1975, Findley 1993).

The specific roost sites selected by various bat species may be determined in part by such factors as morphology, flight and echolocation capabilities, proximity to other resources (food, water, hibernation sites), climatic factors, and roost availability, among others. Vaughan (1970) has reviewed the relation between morphology (skull shape, pelvic girdle, and limb proportions) and roost selection in bats. Shump and Shump (1980) found that hoary and red bats, which roost in exposed locations, have greater pelage insulation than little brown and big brown bats, which roost in more

TABLE 1. Forest canopy use by Pacific Northwest bat species. Species marked with an asterisk (*) are infrequent canopy users; all others listed are regular canopy users.

Species	Canopy Use	
	Roosting	Foraging
Myotis lucifugus[1]	X	X
Myotis yumanensis[2]	X	X
Myotis californicus[3]	X	X
Myotis volans[4]	X	X
Myotis evotis[5]	X	X
Myotis keenii[6]	X	X
Eptesicus fuscus[7]	X	X
Lasiurus cinereus[8]	X	
Lasiurus borealis[9]	X	
Lasionycteris noctivagans[10]	X	X
Plecotus townsendii[11]		X
*Myotis thysanodes**[12]		X
*Myotis ciliolabrum**[13]		X

[1]Barbour and Davis 1969, LaVal et al. 1977, Fenton et al. 1980, Fenton and Barclay 1980, Barclay and Cash 1985.

[2]Fenton et al. 1980, van Zyll de Jong 1985.

[3] Krutzsch 1954 Fenton and Bell 1979, Fenton et al. 1980.

[4] Baker and Phillips 1965, Whitaker et al. 1977, Fenton and Bell 1979.

[5] Manning and Jones 1989, Barclay 1991.

[6]Cowan and Guiguet 1965.

[7] Fenton et al. 1980, Brigham 1991.

[8] Constantine 1966, Shump and Shump 1982, Barclay 1984, Barclay 1985.

[9]Constantine 1966, Furlonger et al. 1987.

[10] Kunz 1982b, Barclay 1985.

[11]Kunz and Martin 1982.

[12]Barbour and Davis 1969, Whitaker et al. 1977.

[13]Fenton et al. 1980, van Zyll de Jong 1985.

protected sites. These authors related pelage differences to differences in roost condition and gregariousness in these species. Hoary bats have a relatively high aspect ratio and wing-loading and are not well adapted for highly maneuverable flight, which may influence their choice of roost sites (Constantine 1966, Barclay 1985). Constantine (1966) found that hoary and red bats generally roost where they could drop down through an unobstructed distance to attain flight speed.

Norberg and Rayner (1987) discuss the relation between morphology, flight, and echolocation capabilities in bats. Tuttle (1976) examined the significance of proximity of maternity roosts to foraging areas and hibernation sites in gray bats (*Myotis grisescens*). Thomas (1988) and Barclay (1991) have suggested that climate and elevation may play a role in the choice of roost location and distribution of the sexes in some bat species.

Choice of roost site may differ with sex, age, reproductive condition, and migratory status of an individual. Constantine (1966) observed that young red bats roost higher in trees than do adults. Fenton (1970) found that reproductive female little brown bats select different roost sites than do males, based upon their thermal requirements.

Most Pacific Northwest species roost in a variety of situations, rather than in only one particular roost type (van Zyll de Jong 1985). The roosting ecology of Pacific Northwest bats has been reviewed by Christy and West (1993).

The major types of tree roosts used by temperate bats include cavities, crevices behind exfoliating bark, crevices formed in rugose bark, cracks in wood, and in foliage. Rarely, bats have been reported roosting in nests of other mammals (squirrels) and in epiphytes (Spanish moss) on trees (Neill 1952, Constantine 1958).

Tree Cavities

Tree cavities used by bats may be in hollows formed in the trunks or branches of snags or damaged live trees. They generally provide a relatively stable microclimate and offer protection from predators (Kunz 1982a, Tidemann and Flavel 1987).

Factors in selecting tree cavities include microclimate, structure, tree age, size, and height.

Microclimate: Microclimate of a cavity can be affected by aspect, entrance height, canopy cover, density of surrounding vegetation, tree status (alive or dead), thickness and insulating properties of the cavity walls, tree diameter, cavity size, and number of bats occupying the cavity. Maeda (1974) found that large noctule bats (*Nyctalus lasiopterus*) in Japan preferentially roost in cavities in live trees, which provides more constant temperatures than cavities in snags. Tideman and Flavel (1987) suggested that the higher water content of live trees increases their insulative value and cavity humidity. Female bats in reproductive condition generally have different breeding-season roosting requirements than males and may roost separately from

them. Pregnant or lactating females often roost colonially at more protected roost sites that provide the high temperatures necessary for maximizing growth and development of the young (Barclay 1991). Males and nonreproductive females commonly roost solitarily or in small groups, in less protected and thermally stable environments (Barclay 1991).

Structure: Maeda (1974) reported that large noctule bats select roosts based on the following structural characteristics of the roost cavity: shape, position, entrance height, size, and degree of entrance protection. The position of the entrance has to permit easy flight from the cavity. Tideman and Flavel (1987) studied cavity-roosting bats in Australia and found that bats select cavities with entrance holes that are just larger than the size of the bat. Presumably, small entrances provide greater protection from predators and may reduce competition from birds and other bats. Roost entrances are also oriented to prevent the entry of rain into the cavity.

Tree characteristics: The age of cavity trees is important to bats to the extent that it is a factor in frequency of cavity formation, cavity size, and cavity characteristics (Tideman and Flavel 1987). Tideman and Flavel (1987) failed to find any relation between roost site selection and tree height, for the Australian bats they studied. Lunney et al. (1988), found that the Australian big-eared bat (*Nyctophilus gouldi) a* cavity- and crevice-roosting species, select large diameter trees, of more than 80 cm d.b.h. for roosting.

Some examples of Pacific Northwest bats known to use tree cavities are the little brown bat (Fenton and Barclay 1980), the big brown bat (Brigham 1991), the California bat (Krutzsch 1954), and the silver-haired bat (Kunz 1982b). Some of these species (particularly the little brown bat, the big brown bat, and the California bat) commonly use buildings as roost sites as well. Barbour and Davis (1969) list buildings as the preferred roost sites for these three species.

Tree Crevices

Many tree-roosting bats roost behind exfoliating bark on trunks or branches of dead or live trees. Bark roosts provide a much less permanent, less secure and less thermally stable roosting environment than cavities. Bats that roost under bark must change roosts more frequently than those roosting in cavities because of the more transient nature of their roost sites (Kunz 1982a). They are probably also more vulnerable to predation and weather.

Other types of crevice roosts include cracks in tree trunks and in larger branches, and crevices created by bark rugosity. Perkins and Cross (1988) reported that silver-haired bats prefer roosting in old (> 150 years) Douglas-fir (*Pseudotsuga menziesii*) forests in Oregon, probably because of the bark characteristics of old trees. The bark of old Douglas-fir tend to provide more crevices by separating more widely from the trunk. Old trees also develop more pronounced ridges and crevices in the bark itself. Bats were found to prefer Douglas-fir to ponderosa pine (*Pinus ponderosa*) and true fir (*Abies* spp.), probably because of differences in bark characteristics. The bark of these latter species tended to be less rugose and generally did not form as deeply creviced furrows. Barclay et al. 1988 observed silver-haired bats roosting in spaces behind folds of bark, in split tree trunks, and in depressions on tree trunks. Other Northwest bats that roost under bark or in other tree crevices include the long-legged bat and the long-eared bat (van Zyll de Jong 1985).

Foliage Roosts

Foliage roosts provide the most exposed type discussed thus far. They are used most frequently in tropical regions. Potential foliage roost sites are more abundant than cavity- and crevice-roosts, but their greater exposure makes them more hazardous. Their abundance, however, makes them easy to find near foraging areas, and might help to reduce commuting distance. The abundance of foliage roosts also facilitates the wide distribution of some foliage roosting species. Predation risks are probably higher for foliage roosting bats, and many temperate and tropical foliage roosters are cryptically colored and roost solitarily or in small family groups (Kunz 1982a). One Northwest foliage roosting species, the hoary bat, has a characteristic grizzled appearance that may contribute to its concealment. Temperate foliage roosting species are generally well insulated against cold temperatures (Shump and Shump 1980) and may make long distance latitudinal migrations in response to diminished winter food supplies (Shump and Shump 1982).

Foliage roosting bats tend to change roosts more frequently than other species in response to the transient nature of their roost sites. Within the

same season, they may show some fidelity to a general area, however (Kunz 1982a, Lunney et al. 1988).

Bats that roost in foliage may roost high in the canopy, in subcanopy trees, or in understory foliage. Roost sites may be in dense foliage, in relatively exposed locations, among leaves, or on branches. Sites may be concealed from above, but conspicuous from below (Constantine 1966, Kunz 1982a). Hoary bats and red bats (*Lasiurus borealis*) for example, have been found to select roost sites covered by dense foliage above and around the sides, but open below. This arrangement presumably reduces their visibility and accessibility to predators, but permits them to take flight readily (Constantine 1966).

Location of the roost tree relative to surrounding vegetation may also be of importance to some species. Certain species may prefer trees within the forest interior, and other species prefer to roost along a forest edge. Constantine (1966) reported that hoary and red bat roost sites were usually located along a forest edge.

Perkins and Cross (1988) found that hoary bats were primarily associated with old Douglas-fir forests in Oregon and hypothesized that this is due to bats' roosting requirements. The large trees and large and heterogeneous canopies found in such forests may furnish more roost sites available for foliage roosting bats than young forests. Old coniferous forests are more likely to provide the canopy structure, including dense foliage adjacent to uncluttered flight space, required for roosting by these bats. In contrast to younger trees, older trees tend to have crowns that begin higher off the ground and have the needles more concentrated toward the edge of the canopy (Perkins and Cross 1988).

Foraging

Foraging tends to be opportunistic rather than restricted to a particular foraging strategy or habitat for most North American bat species (Vaughan 1980, Barclay 1991, but see Fenton 1982, Furlonger et al. 1987). Furlonger et al. (1987) found that bats in eastern Canada exploit concentrated patches of prey. They suggested that this type of foraging strategy may supersede preference for a particular type of foraging habitat. Some authors (Black 1974, Crome and Richards 1988, Findley 1993) maintain that species of bats may partition foraging habitat by vegetation structure, reflecting differences in their morphology, echolocation call structure, and flight capabilities. Findley (1993) reviews the relation between morphology and community structure in bats.

Foraging Habitat

Aldridge and Rautenbach (1987) divided African insectivorous bats into four major groups according to foraging-habitat preference: (1) clutter foragers, maneuverable species with echolocation calls suited to a cluttered environment and capable of foraging within the forest canopy; (2) intermediate clutter foragers, moderately maneuverable bats capable of foraging in open areas and open woodland, but not within dense vegetation; (3) woodland-edge foragers; and (4) open-air foragers that lack maneuverability. Other authors have used similar classification schemes to describe North American bat species. LaVal et al.(1977) studied bat populations in Missouri and found that hoary and red bats tended to forage in open areas away from forest clutter, including high over the forest canopy and over open fields. Gray bats foraged in riparian areas and over water. Little brown bats foraged along forest edges and within the forest. The northern myotis (*M. septentrionalis*) a close relative of the Keen's myotis, a Pacific Northwest species, was a clutter forager and foraged in forested areas. The Indiana myotis (*M. sodalis*), another clutter forager, foraged primarily in the canopy, but the northern myotis foraged below the canopy but above the understory shrub layer, which suggests that some vertical stratification may occur within bat communities.

Crome and Richards (1988) investigated the differential use by bats of gaps (created by logging) and closed canopy areas in an Australian rain forest. They divided bat species into canopy specialists (clutter foragers), gap incorporators (intermediate clutter foragers), and gap specialists (open-air foragers). Habitat preference of the bats was found to be related to wing morphology and flight maneuverability. Canopy-specialists were highly maneuverable, and gap specialists were capable of faster but less maneuverable flight. Gap incorporators, which foraged in both types of habitats, had wing characteristics and flight capabilities intermediate between the other two types. Crome and Richards (1988) concluded that vegetation structure and wing morphology determine allocation of different habitat types among species.

Many Pacific Northwest species forage in riparian areas (little brown bats and Yuma bats (Kurta 1982, Herd and Fenton 1983, Lunde and Harestad 1986, Brigham et al. 1992), in clearings and roads within forests (California bat, Yuma bat, and long-legged bat (Barbour and Davis 1969, Fenton and Bell 1979, Brigham et al. 1992) or in open areas or along forest edges (hoary bat, red bat) (Constantine 1958, Barclay 1985). Gleaning species, such as the long-eared bat and possibly the Keen's bat, may forage within the canopy (Cowan and Guiguet 1965, Manning and Jones 1989, Barclay 1991). None of these species are known to restrict its foraging to just one habitat type, however. Riparian areas and forest edges are exploited by many bat species to some extent, perhaps because these areas support higher densities of flying insects (Furlonger et al. 1987, Cross 1988, Thomas 1988, Barclay 1991).

Landscape Context

Although several canopy attributes may be of consequence to bats (Carey, this issue), the composition of the surrounding landscape may also play a role in determining the relative importance of specific attributes, and may influence bat distribution. Some landscape-scale considerations are discussed below.

Distribution of Bats

Several authors have looked at the diversity of bat communities in different broad habitat types. In general, topographically complex regions tend to support the most bat species. Jones (1965) studied bats in the Mogollon Mountains of New Mexico and Arizona. He recorded the greatest percentage of captures in higher elevation, mixed-conifer, forest; an intermediate percentage in mid-elevation, pine-oak woodland; and the lowest number of captures in lowland, xeric-shrub, grassland. These differences were presumably related to differences in availability of roost sites, food resources, and water. Jones (1965) found that different species dominate the bat community in each of these habitats. Big brown bats predominate in higher elevation coniferous forest, and hoary bats are most common in the pine-oak woodland.

Thomas (1988) found a disproportionate use of old-growth Douglas-fir stands by bats in the Cascade Range of Washington and Oregon and Coast Ranges of Oregon, compared to young and mature stands. Increased roost availability in old growth stands probably accounted for this difference because bats did not appear to be concentrating foraging activity within the forest stands.

Resource Proximity

Although forest bats may have roosts that meet their primary requirements within a particular forest stand, the composition of the surrounding landscape is important in determining whether roost sites can be used successfully. Proximity of good quality roost sites to foraging and drinking areas, as well as to hibernation sites, can reduce the energetic costs of commuting (Tuttle 1976). Because many bats concentrate their foraging in riparian areas, proximity of roost sites to riparian areas assumes particular importance. Where roost sites are far from foraging areas, juvenile mortality may be higher. Tuttle (1976) found that growth and survival of juvenile gray bats in the southeastern United States is impaired when the distance from the maternity roost site to foraging areas is too great. Optimal maternity-roost conditions, highly productive foraging sites, and nearby hibernation sites can compensate for greater roost-to-foraging site distances, however (Tuttle 1976).

Bats sometimes may require connecting corridors of suitable habitat between critical resources. Tuttle (1976) observed that gray bats, which roost in caves and forage over water, generally fly between these sites within the forest canopy.

The abundance, diversity, and relative proportion of critical resources may also be important to bats. Many bats change roosts frequently and require several different roosts of diverse character to compensate for changes in air temperature, weather, predators, prey patches, and other factors. Humphrey et al. (1977) observed a maternity colony of Indiana bats that used two roost sites about 30 m apart. Each roost site had different thermal properties, and the colony shifted between them depending on temperature and weather conditions. Bats may therefore need a selection of different roost sites (and perhaps different tree species), with a variety of thermal and other properties, distributed across the landscape and located within a fairly constrained area.

Riparian Zones

As is true for many other vertebrates, riparian zones assume disproportionate importance for many bats,

which may do most of their foraging in these insect-rich areas (Brigham et al. 1992). Bats frequently use riparian zones as travel corridors as well. Thomas (1988) found that foraging rates for several Pacific Northwest *Myotis* species are significantly higher over water than in the forest where they roost. Roost sites may be more abundant in riparian areas because of an increased number of snags and older trees, as well as rock crevices in eroded stream banks (Cross 1988). For species such as the hoary bat, known to roost in deciduous trees, riparian areas may be preferred because of a preponderance of such trees in the riparian zone (Cross 1988). Riparian areas also provide the open flight space and forest edge conditions required by some species.

Role in Forest Ecosystems

Tree-roosting bats, which deposit large amounts of nitrogen-rich guano at the roost site, may help to provide nutrients in forest ecosystems with nutrient-poor soils. Given their great mobility, bats may be important in transporting nutrients from riparian areas or locations outside the forest ecosystem into forest communities (Cross 1988, Rainey et al. 1992).

Continuous occupation of cavity roosts by bats may modify the roost substrate and environment in ways that affect other cavity dwellers. These effects may include erosion of cavity sides, increased humidity, increased ammonia, increased temperature, and an enhanced rate of deterioration of the roost tree by the accumulation of feces and urine (Kunz 1982a).

Bats consume many insects, such as termites, that are considered to be forest pests (Whitaker et al. 1977). Their role in controlling forest pests remains to be determined, however.

Conclusion

Bats are a highly diversified taxonomic group whose small size, low reproductive rate, high energy demand, and complex needs have made them, perhaps, more vulnerable than many other vertebrate groups. These complex needs require a complex environment. Tall canopies and diverse forest structure, such as those found in late seral stages of coniferous forests may provide some of the complexity needed by bats (Perkins and Cross 1988). For many bat species, a mosaic of habitat types in close proximity to one another, including a mix of forests, openings, and riparian areas, may provide optimal habitat.

A tremendous amount of research remains to be done to assess the role of forest canopies in Pacific Northwest bat communities. The relative importance of the canopy attributes described in Carey (this issue), including such factors as layering, degree of canopy closure, gaps, canopy volume, and tree species characteristics, need to be investigated. Much of the information currently available is anecdotal, often based on unproven assumptions, or represents generalizations derived from knowledge of bat communities elsewhere. Additional data are needed on roost availability vs. use, insect densities, and prey selection by bats in the canopy and in forest gaps, and effects of landscape composition on bat behavior. Effective management for bats in the Pacific Northwest will require basic research on forest canopy and landscape use. This type of information should prove valuable for making management decisions on cavity tree retention, creation of multilayered canopies, and riparian zone protection.

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The Biologically Significant Attributes of Forest Canopies to Small Birds

Abstract

The biologically significant attributes of Pacific Northwest canopies to passerines and other small birds are reviewed. Some evidence suggests that deciduous and coniferous forests represent basic criteria for broadscale habitat selection of PNW birds in this region. However, many species possess rather generalized habitat affinities, and are adapted to a variety of forest types and stand ages. Fine-scale habitat discrimination appears to be associated with structural features such as branch architecture, bark texture, percentage vegetation cover, snag characteristics, and the density and the geometry of foliage. Many species of birds, particularly cavity nesters, reach their greatest abundance in old forest types. Old-growth forests have also been shown to provide important wintering habitat for several birds that reside here permanently. Riparian communities represent another special vegetation type characterized by high avian abundance and species richness.

Introduction

Songbirds are frequently used to characterize forest communities, because they are useful indicators of habitat quality and provide insight into the carrying capacity of various habitats (Graber and Graber 1976, Gilbert and Allwine 1991). Passerines are particularly suited for field censusing because they are diurnal, abundant, easily detected, and possess diverse life histories (Paulson 1992). In the Pacific Northwest, most research on forest avifuana has examined abundance and distributional patterns in various forest types and stand ages, or in relation to structural features such as snags and gaps. In general, however, the basic biology of many species has not been adequately documented, particularly in relation to how birds use canopy environments across the varied topographical, moisture, and vegetational gradients that characterize these forests. The objective of this paper is to provide an overview of how Pacific Northwest canopy ecosystems are relevant to the biology of the region's small, forest-dwelling birds (i. e., passerines, swifts, and woodpeckers). Structural attributes of these systems are emphasized.

Historical Perspective

Forest vegetation has changed dramatically over the last 30,000 years in response to large scale changes in the Earth's climate (Brubaker 1991). Consequently, Douglas-fir (*Pseudotsuga menziesii*) forests probably do not represent a co-evolved complex of species bound together by tightly linked and balanced interactions (Brubaker 1991). This inference provides insight into why most Pacific Northwest birds are generalist foragers, because insufficient time has elapsed for them to segregate into small exclusive niches (Orians and Wilson 1964, Slobodkin and Sanders 1969, Gilbert and Allwine1991). Airola and Barrett (1985) found that permanent residents in the Sierra Nevadas made greater use of substrates that were available year-round, such as conifer foliage, branches, and tree trunks than seasonally available substrates. Presumably this difference reflects their adaptation to northern coniferous landscapes (Mayr 1976), and the need to retain efficient foraging abilities on substrates during the winter when prey is scarce (Sabo and Holmes 1983). In contrast, Airola and Barrett (1985) found that most migrants preferred the more productive, seasonal, deciduous vegetation characteristic of neotropical areas for where they are derived (Mayr 1976). A similar pattern of foliage-type preference was also noted by Alatalo (1982) in northern Finland, who found that migrants used more of deciduous foliage then did residents. Research on the Olympic Peninsula (Sharpe, unpublished data) also supported these foliage-type preferences by demonstrating that most resident species used coniferous forests as their primary habitat, but the region's migrants exhibited a broader use of forest communities including deciduous, mixed and coniferous communities. Such differences in foliage-type preferences, however, are relative (Airola

and Barrett 1985), and their several migratory species make extensive use of coniferous forests; the olive-sided flycatcher (*Contopus borealis*), western wood pewee (*Contopus sordidulus*), hermit warbler (*Dendroica occidentalis*).

Tree Species Composition

The factors associated with habitat selection by birds are not well understood. Avian habitat selection may be hierarchically ordered, proceeding from gross physiognomic features at the regional scale to specific vegetation types at more localized scales (Wiens and Rotenberry 1981, Klopfer and Ganzhorn 1985). At fine scales, habitat discrimination appears to be associated with structural features such as branch architecture, bark texture, percentage vegetation cover, snag characteristics, and the density and geometry of foliage (Robinson and Holmes 1982, Raphael and White 1984, Airola and Barrett 1985, Holmes and Schultz 1988). Preferential use of specific tree species is well documented for cavity nesters in the Pacific Northwest (Mannan et al. 1980, Raphael and White 1984, Manuwal and Huff 1987, Holmes and Schultz 1988, Nelson 1988, Manuwal 1991). Several studies in temperate systems also demonstrate that insectivorous birds forage for their prey differentially among the foliage of various tree species (Franzreb 1978, Hunter 1978, Bushby and Sealy 1979, Holmes and Robinson 1981, Airola and Barrett 1985, Morrison et al. 1985). Robinson and Holmes (1984) have also shown that some birds change their search tactics when foraging on different tree species. Holmes and Schultz (1988) have also suggested that the availability of food resources for foraging birds are a function of the type and abundance of prey species present, which varies among tree species; the foliage structure and characteristics of the trees, which influence prey detectability and accessibility; and the morphological and behavioral abilities of each bird species to perceive and capture those prey. The following paragraphs provide some examples of how the structure and substrate of canopies interact with prey and avian morphology to determine food availability for birds.

One of the most obvious differences between conifer and deciduous trees is the type of food resources they produce. Conifers produce seed crops (favored by nuthatches, finches, and crossbills) and broadleaf vegetation generally produces fruits and nuts (favored by such birds as waxwings, tanagers, and thrushes). Perhaps equally important, but more difficult to quantify, is the manner in which the contrasting structural environment of conifers and evergreens influence the foraging activities of songbirds. Compared to deciduous trees, evergreens typically provide continuous cover and a more ameliorated microclimate for both arthropods and foliage-gleaning insectivores (Axelrod 1966, Jackson 1979). In the Sierra Nevada, Airola and Barrett (1985) found that ridged, horizontal limbs of conifers were favored by perch-gleaning insectivores, which could hop along branches, and access large amounts of foliage. The xerophytic nature of conifer needles (Jackson 1979), however, and the presence of secondary compounds in certain conifer species (Wahlenberg 1946) may limit the exploitation of evergreens by phytophagous insects, which may subsequently limit insectivorous birds. For example, Airola and Barrett (1985) found that, during the nesting season, insectivores avoided feeding on incense cedar (*Calocedrus decurrens*), which they attributed to the tree's essential oils, in addition to the small, scale-like needles that mature quickly and reduce the period of susceptibility to phytophagous insects. In contrast, Morrison et al. (1989) found that brown creepers (*Certhia americana*) concentrated their foraging activity on incense cedar during the winter in response to the seasonal availability of scale insects. Ecomorphological studies by Leisler and Thaler (1982) and Keast and Saunders (1991) found that the papillae on the feet of the golden-crowned kinglet (*Regulus satrapa*) penetrated the rugosities of conifer foliage and twigs, allowing the bird to adopt feeding postures and take advantage of foraging opportunities that are more difficult for its smoother-footed congeneric, the ruby-crowned kinglet (*R. calendula*). Several studies have suggested that the foliage structure of deciduous trees can influence how insectivorous birds detect, attack, and capture prey. For example, some deciduous trees may require small, perch-gleaning birds to expend more energy accessing the leaves, which are typically at the ends of branches (Robinson and Holmes 1982). Franzreb (1978) has also suggested the large size and movement of the leaves of quaking aspen (*Populus tremuloides*) may limit the ability of ruby-crowned kinglets to exploit them as a foraging substrate. Birds that are capable of hover-gleaning, however,

can probably access larger leaves, and they are therefore less constrained by branch and foliage structure (Holmes and Robinson 1981). Whelan (1989), however found no effect of tree species on the learning rates of two eastern paruline warbler species, suggesting that these birds should be able to respond to prey distribution changes equally well on both sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*).

The surface texture of tree trunks is also important to birds belonging to bark-gleaning and trunk-drilling guilds. In general, the abundance and availability of bark arthropods increases on larger diameter, more heavily furrowed trees (Jackson 1979, Morrison et al. 1985, Nicolai 1986) and is correlated with an increase in brown creepers and, to a lesser extent, red-breasted nuthatches (*Sitta canadensis*) in older stands (Mariani and Manuwal 1990, Huff et al. 1991). In addition, birds such as black-capped chickadees (*Parus atricapilis*) and pine siskins (*Spinus pinus*) have been found to use foliage damage caused by phytophagous insects as cues to locate prey (Heinrich and Collins 1983, Roland et al. 1986).

Gaps

Forest openings caused by natural tree mortality are a conspicuous feature of late-successional forests (Franklin et al. 1981), and are typically characterized by heightened avian richness and abundance. Higher light levels penetrate to the forest floor in gaps, resulting in an increased concentration of resources for birds, such as fruit-bearing deciduous shrubs and insects (Blake and Hoppes 1986). Aerial-sallying insectivores such as flycatchers and tanagers also appear to be influenced by small gaps, since their feeding activities often occur in interior spaces within the canopy (Airola and Barrett 1985, Gilbert and Allwine 1991). Gaps may also influence the vertical distribution of birds in the canopy, as some species that dwell high in the crown move down to lower levels in gaps (Airola and Barrett 1985, Balda 1969).

Canopy Height

As tree height increases, there is a concomitant increase in vertical profiling and selective use of the canopy by birds. Hawking and sallying species such as warblers and flycatchers appear to favor open sites higher in the canopy where there is increased visibility and maneuverability (Airola and Barrett 1985). Foliage gleaners have also been found to focus their foraging activity on leaves that have recently been exposed to sunlight, as these newly-warmed surfaces are presumably sites of increased insect activity (Balda 1969, Airola and Barrett 1985). In contrast, trunk gleaning species such as the red-breasted nuthatch and brown creeper favor lower, older portions of the canopy where furrowed bark is more abundant (Jackson 1979, Airola and Barrett 1985, Morrison et al. 1989).

Snags

Snags are important structural features of Pacific Northwest forests (Cline et al. 1980, Franklin et al. 1981) and are used extensively by resident birds for cavity nests, roosting, perch hunting, and as a foraging substrate. Consequently, the absence of standing deadwood structures can be a major limiting factor for many snag-dependent birds (Haapanen 1965, Balda 1975, Cline et al. 1980, Raphael and White 1984). Nearly all cavity nesting birds in these forests prefer to excavate their nests in dead wood or dying trees rather than live trees (Raphael and White 1984, Lundquist and Mariani 1991). Several studies have also demonstrated that most cavity nesters select the tallest and largest diameter snags within a stand (Mannan et al. 1980, Raphael and White 1984, Zarnowitz and Manuwal 1985, Carey et al. 1991). These larger-diameter snags confer several advantages to nesting birds, including increased thermal insulation, enhanced protection from predators, and more room to house large clutches (Karlsson and Nilsson 1977, Pingjun and Martin 1991). Food resources for birds also increase with larger diameter snags because of their increased surface area for wood boring insects, as well as their greater moisture retention, which is favorable for termites (Blackman and Stage 1924). Larger diameter snags, particularly those species with slower decay rates, tend to persist longer and thus increase their value to birds (Dahms 1949). Nelson (1988) found that the relatively soft, ephemeral snags of western hemlocks were avoided by all species of cavity nesters. Birds may also avoid hemlock, or well-decayed snags of any species, because the soft wood may compromise the integrity of the nest entrance and increase the risk of predation. Soft snags may be more susceptible to breaking at the cavity during high winds (Pingjun and Martin 1991). Birds also tend to favor snags that are clustered on the landscape, because clustering reduces the amount of time spent traveling between food

patches, as well increasing the search costs for predators (Raphael and White 1984, Pingjun and Martin 1991).

Non-cavity nesting species such as flycatchers and raptors often use snags rather than live stems for perching and hunting sites. Once snags have toppled, they continue to be used by birds as song perches, plucking posts, and drumming posts. Decaying woody debris also supplies important habitat for invertebrates and small mammals, which in turn provides food for forest birds.

Stand Age

Several studies have examined changes in bird communities across a chronosequence of naturally regenerated stands that include young, mature, and old-growth forests (Manuwal and Huff 1987, Carey et al. 1991, Gilbert and Alwine 1991, Huff and Raley 1991, Lundquist and Mariani 1991, Manuwal 1991). In general, these studies found avian diversity to be relatively consistent across a chronosequence; however, abundance was highest in old-growth stands older than 200 years for many species of birds. Mature stands (80 to 200 years old) generally exhibited lowest abundance, which was attributed to the uniform canopy, poorly developed understories, and the limited availability of large snags. Young stands (about 30 to 90 years old) in contrast, often had snags or large stumps as carry-overs from a previous late-successional forest, and these structures provided nest sites for species such as chestnut-backed chickadees (*Parus rufescens*).

Nesting species that have been found to reach their greatest abundance in old forests types include the hairy woodpecker (*Picoides villosus*), red-breasted sapsucker (*Sphyrapicus ruber*), pileated woodpecker (*Dryocopus pileatus*), Pacific-slope flycatcher (*Empidonax difficilis*), olive-sided flycatcher (*Contopus borealis*), red-breasted nuthatch, winter wren (*Troglodytes troglodytes*), brown creeper, chestnut-backed chickadee, varied thrush (*Ixoreus naevius*), hermit thrush (*Catharus guttatus*), red crossbill (*Loxia curvirostra*), and evening-grosbeak (*Coccothraustes vespertinus*). The Vaux's swift (*Caetura vauxi*), however, is associated exclusively with old-growth forests for nesting and roosting snags (Bull 1991). Franklin et al. (1981) demonstrated that old-growth forests have several ecological attributes limited or absent in younger stands, including large old trees, snags, canopy gaps, increased foliage-height diversity, high foliar biomass, high leaf surface area, and a mixture of tree species and age classes. Stiles (1980) also demonstrated that older forest communities, with their increased vertical profile, permit birds to nest higher above the ground than in younger stands. Consequently, they can have spherical territories, an optimal shape for reducing energy expenditures associated with foraging trips and territorial defense. Old growth also provides critical wintering habitat for the relatively large percentage of permanent residents in the Pacific Northwest (Manuwal 1991). Research on winter birds by Manuwal and Huff (1987) and Huff et al. (1991) in young, middle-aged, and old-growth stands has demonstrated that older forests provide more suitable winter habitat by providing more food resources and an ameliorated microclimate for roost sites. Consequently, more birds survive the winter in older stands and may replenish younger stands in the spring. Western hemlock, a prolific seed producer, is a shade-tolerant species that is dominant in many older stands (Franklin and Dryness 1973, Franklin et al. 1981). Compared to other species, such as Douglas-fir, hemlock becomes important for wintering finches by providing a more stable intra-annual production of cone crops as well as delayed release of seeds, which supplies a food resource lasting into the cold winter months (Isaac 1943, Fowells 1965, Manuwal and Huff 1987).

Riparian Communities

Riparian communities represent another special vegetation type receiving extensive use by birds, particularly in drier regions. These systems occupy a unique link between aquatic and terrestrial habitats and consequently provide a localized abundance of food, water, and cover for birds and other wildlife (Odum 1979, Oakley et al. 1985, Naiman and Decamps 1990). Noteworthy features of riparian areas include the high edge-to-area ratios of stream corridors, and the unique disturbance regime of flowing water, which creates a mosaic of plant communities and stand ages (Campbell and Franklin 1979, Thomas 1979). In addition, riparian communities are frequently characterized by structurally complex vegetation with large snags and live trees because of the optimal growing conditions and year-round availability of water (Campbell and Franklin 1979, Oakley et al. 1985). These conceptual values are well recognized in drier regions where the vegetational gradients

between riparian systems and upland communities is very pronounced (McGarigal and McComb 1992). In the moist coniferous forests west of the Cascade Mountains, however, the differences between riparian areas, particularly along small streams, and upland communities is less dramatic, and consequently the changes in avifuana between these two systems is much less obvious (Anthony 1984, Bruce 1985, Carey 1988, McGarigal and McComb 1992). Even along small streams, however, some evidence has been found that songbirds, such as as the black-throated gray warbler (*Dendroica nigrescens*), MacGillivray's warbler (*Oporornis tolmiei*) and the wrentit (*Chamaea fasciata*) are associated with the presence of water (Carey 1988). The value of small streams may be associated with their steep gullies or ravines, which facilitate tree fall and the development of gaps and deciduous understories (Carey 1988). As stream size increases, their value to songbirds also increases significantly. For example, Lock (1991) was able to demonstrate on the Olympic Peninsula that higher avian richness and abundance were found on large-order rivers. Perhaps the importance of riparian communities is best exemplified by the disappearance of the western subspecies of the yellow-billed cuckoo (*Coccyzus americanus occidentalis*), whose disappearance from most of western North America is attributed to loss of contiguous tracts of cottonwood-willow riparian woodland (Laymon and Halterman 1987).

Managed Forests

Avian use of commercial forests often contrasts sharply with use of naturally regenerated stands. Managed forests are typically characterized by much larger areas of disturbance and a simplification of forest structures that includes reduced density of snags, woody debris, and live trees. Initially, some resources are available for forest birds in large clearcuts, and consequently these sites are often used by open-country birds like hummingbirds, nighthawks, shrikes, and sparrows. If critical wildlife features are retained, however, the avian diversity of managed areas may surpass that of the late-successional forest that formerly occupied the site. Note, however, that essentially all of the species that use harvested areas are cup-nesting species belonging to ground-, brush-, or nectar-foraging guilds, and thus do not present the conservation concerns of forest interior species such as the Vaux's swift, spotted owl (*Strix occidentalis*), goshawk (*Accipter gentilis*), and marbled murrelet (*Brachyramphus marmoratus*). Studies by Martin (1981) and Rosenberg and Raphael (1986) in western forests found that resident birds, or birds with large home ranges and restricted habitat requirement were the most sensitive to forest fragmentation. Separating the impacts of timber harvest into those associated with edge effects and those associated with the direct loss of habitat can be difficult, however.

Future Research

Despite the considerable body of research that has been conducted on the region's avifuana, several areas need more study. A more detailed understanding should be developed as to how each bird species modifies its use of canopy environments in response to the complex topographical, moisture, and vegetational gradients that characterize each of the subregions in the Pacific Northwest. Although considerable attention has been devoted to cavity-nesting species, we need more information on the habitat selection, nesting requirements, and foraging behavior of non-excavating passerines. Much remains to be discovered about the population status of neotropical migrants and the relative contribution of habitat loss in the sub-tropical winter areas compared with Pacific Northwest forests. Ecosystem management offers many promising management options that address the conservation needs of the region's avifuana; however, these techniques need to be examined with long-term studies. A better understanding is needed of the effects growing human populations have on avian communities, particularly at the interface between urban/residential areas and forest environments. Attention should be focused on specialized forest types, such as riparian communities and Garry oak systems, where most declines and localized extirpations of Pacific Northwest avifuana have occurred (Hunn 1982, Lewis and Sharpe 1987, Paulson 1992).

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Northern Temperate Coastal Sitka Spruce Forests with Special Emphasis on Canopies: Studying Arthropods in an Unexplored Frontier

Abstract

Arthropod biodiversity is being investigated in the Carmanah Valley on Vancouver Island, British Columbia. Examination of several species, many of which are not yet described from this intact old-growth forest indicate that this structurally complex habitat acts as a reservoir for biological diversity. Nowhere is this more apparent than in the canopy, where the fauna has finely partitioned the tree, both with regard to habitat type and phenology. Resident arthropods associated with the branches in the canopy are dominated by members of the phytophagous and predator/parasitoid guilds. Microhabitats exploited by this arboreal arthropod fauna are not replicated in any of the other forest sites that we examined. Taxonomic distinctness is most pronounced in the moss mats where soil microarthropods such as oribatid mites are members of a unique arboreal community. Removal of this habitat may change the structural and functional aspects of this canopy ecosystem and initiate species extirpations. Intact northern temperate coastal old-growth forests are also important for the maintenance of biodiversity of certain ground-dwelling groups of insects such as the Staphylinidae. These beetles do not easily make the transition to altered habitats. Other insect groups such as the highly mobile spheciform wasps appear to adjust to habitat changes that are most commonly a result of forest clearing. These data indicate that old-growth forests have distinct species assemblages that are altered when forests are converted to younger stands; this is particularly evident in the resident canopy community.

Introduction

Historically very little research concerning the maintenance and conservation of biodiversity has been done on the primeval old-growth conifer forests of the Pacific Northwest. In British Columbia these forests are thought to contain much of the biodiversity of the province (Fenger and Harcombe 1989; Bunnell 1990). They often have diffuse boundaries with other ecosystems, and this temporal and spatial mosaic creates a dynamic and complex set of habitats that are utilized by a variety of species.

The elements of biodiversity associated with old-growth forests form a heterogeneous group, and nowhere is this more evident than in the arthropods. Arthropods, primarily insects, are an integral part of any old-growth system and most entomologists agree that they may comprise 80-90% of the total known species in these systems (Asquith et al. 1990). They play a primary role in the function of natural ecosystems and are now frequently mentioned as important components of diversity that need to be identified (May 1986). As Platnick (1991) states "Speaking about biodiversity is essentially equivalent to speaking about arthropods. In terms of number of species, other animal and plant groups are just a gloss on the arthropod theme." The Entomological Society of Canada also passed a resolution concerning the study of biodiversity of terrestrial arthropods in 1991.

The diversity of arthropods and ecological concepts surrounding them has the potential to bury researchers in a profusion of special cases (Hoekstra et al. 1991). Nowhere is this more obvious than with the insect fauna where species estimates ranged from 1.5-1.8 million species (Hammond 1990) to 30 million species (Erwin 1983), or even up to 80 million species (Stork 1988). The truth probably lies somewhere between these estimates e.g. approx. 10 million (Erhlich and Wilson 1991), but our knowledge of almost all insect faunas is very incomplete. This lack of knowledge certainly applies to the Canadian insect fauna where 33,755 species of insects have been described, although the estimated total number is over 66,000 (Danks 1993). In British Columbia there may be as many as 40,000 arthropod species, many of which are not yet described (Cannings 1992). Community structure of forest arthropods, therefore, is not well known and information concerning responses of these communities to forest management practices is lacking (Schowalter 1985,1986,1989; Schowalter and Crossley 1987).

Within these forest systems one of the least explored habitats is the forest canopy. Insect assemblages in forest canopies are complex in terms of diversity, species interactions, host plant associations and abiotic gradients. The role of these variables in determining community structure of forest insects in general is discussed by Strong (1974 a, b) and previous studies have concentrated on responses of individual species (Dyer 1986; Schowalter et al. 1986; Witcosky et al. 1986) rather than with interactions at the community level.

The canopy of rainforest trees (particularly in the tropics) is believed by many to hold the key to the immense diversity of insects. Indeed this biotope has recently been described as "the last biological frontier" (Erwin, 1983). Although much has been learned in recent years about canopy insects (mainly species lists) in tropical rainforests, relatively little is known about northern temperate rainforests. Canopy research in these forests lag behind tropical canopy studies and only three studies of old-growth forest-canopy invertebrates in the Pacific Northwest had been completed by 1989 (Voegtlin 1982; Schowalter 1986, 1989), and these were carried out in the context of old-growth Douglas Fir-Hemlock surveys in Oregon.

Given the importance of arthropods in old-growth forests of the Pacific Northwest and the lack of taxonomic knowledge, the objective of this study is to document the arthropod fauna from an old-growth Sitka spruce forest and look at species changes along a gradient from the old- growth forest canopy to a second-growth forest. Specifically, this paper will look at guild structure and the microarthropods associated with the forest canopy. Between-habitat species composition of the Staphylinidae (Coleoptera) and the Spheciform wasps (Hymenoptera) will be used as examples to document species compositional changes associated with habitat alterations.

Methods and Materials

Study Area

The study area is located in the Upper Carmanah Valley drainage on the Southwest coast of Vancouver Island, British Columbia, Canada (Figure 1). This typical U-shaped coastal valley, approximately 6731 ha. in extent, is situated between the villages of Port Renfrew and Bamfield. The entire valley lies within the Coastal Western Hemlock Biogeoclimatic Zone with the exception of two high-elevation areas (Meidinger and Pojar 1991). The dominant conifers in the Carmanah drainage are Sitka spruce (*Picea sitchensis*) (Bong.) Carr., western hemlock (*Tsuga heterophylla*) (Rafn.) Sarg., western red cedar (*Thuja plicata*) D. Don and Pacific silver fir (*Abies amabilis*) (Dougl.) Forb.

The sample area in the Upper Carmanah Valley (UTM: 10U CJ 801991) includes 6 study sites: old-growth canopy (UTM: 10U CJ 801991), old-growth forest floor (UTM: 10U CJ 802998; both old growth sites are approximately 300-500 years old), transition zone (edge between old-growth and clear-cut; UTM: 10U CJ 803006), clear-cut (UTM: 10U CK 803005), second-growth 1 (UTM: 10U CK 803000) approximately 10 years old and second-growth 2 approximately 60 years old. All study sites except the 60 year old site were located adjacent to one another along an approximately 4 km transect. This watershed represents an intact ancient forest that has been evolving since the Wisconsin glaciation. In 1985 the clear-cut site, (approx. 4 hectares) was harvested and is the only area in the entire Carmanah watershed to be logged. The 60 year old site located along the Rosander mainline, is not contained in the Carmanah Valley watershed and lies 30 km to the southeast from the Upper Carmanah Valley.

Canopy Access

Five Sitka spruce trees were randomly chosen to be incorporated into the access system. Access to the Sitka spruce canopy is by means of a 2:1 mechanical advantage pulley system. Strapped into a harness and attached to a series of climbing lines, we are able to sample five adjacent Sitka spruce trees. Four wooden platforms strapped onto the branches and trunk of the main tree give us consistent heights (31 to 67 metres) from which to sample. A series of burma bridges enables us to access four other Sitka spruce trees, complete with platforms. This entire system, the first of its kind in North America, has become a springboard for documenting old-growth forest arthropods. At the time of study this station was the only permanent access system of this type available to do long-term canopy work in Northern temperate rainforests.

A second permanent access station was completed in March, 1994, near Victoria, B.C. allowing

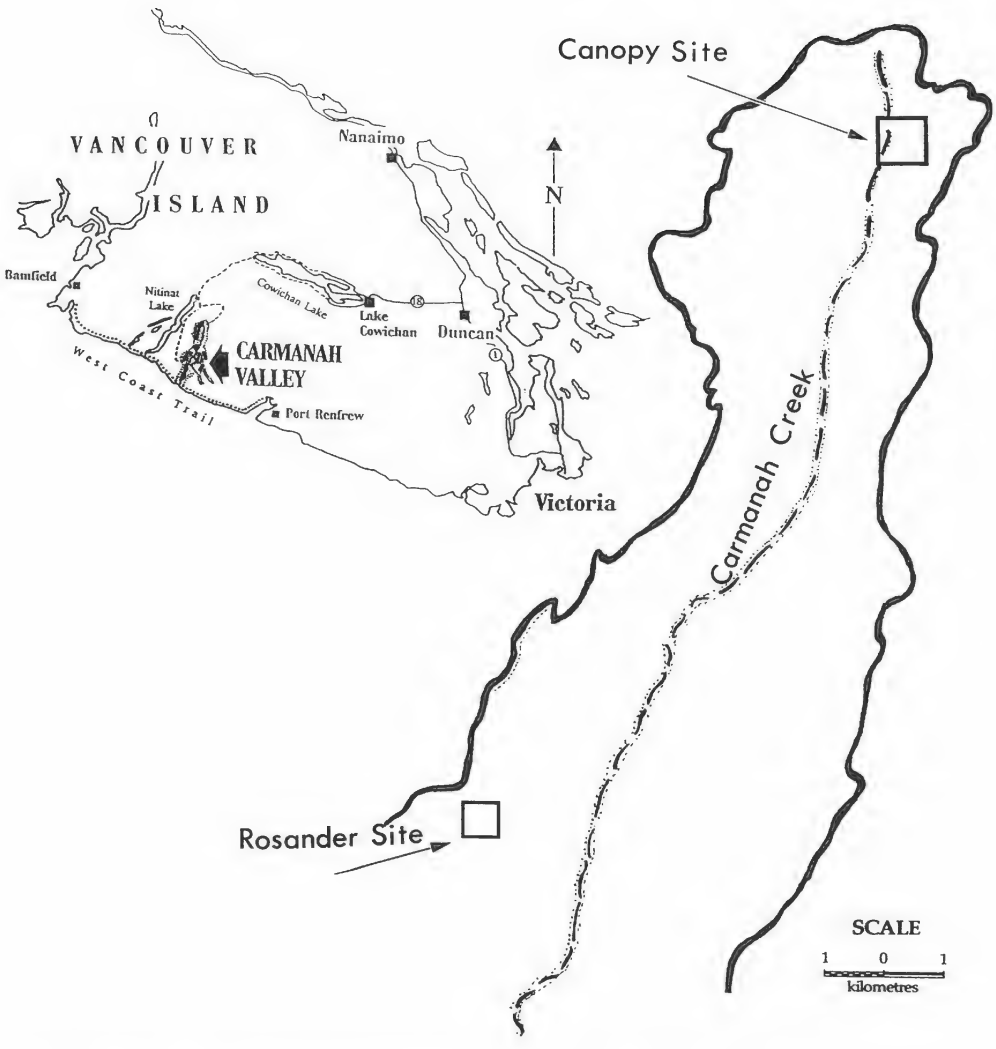

Figure 1. Map location of the study sites in the Carmanah Valley, Vancouver Island, British Columbia, Canada.

access to a dry coastal old-growth Douglas fir forest, and a third has been completed recently (May, 1994) in old-growth western red cedar at Bamfield Marine Station, B.C.

Survey Design

Arthropods (mainly insect, mites and spiders) have several biological features that predispose them to diversity in response to environmental heterogeneity (Southwood 1978). The ability of insects to exploit a variety of habitats coupled with their diversified behaviour means that few, if any, traps are equally efficient in capturing different groups. Owing to the diverse nature of the taxa involved in an arthropod biodiversity study coupled with their varied habits and life cycles, no single survey method or sampling technique can be used for a complete study. A variety of techniques must be employed and the sampling techniques that are most easily used, and the relevant taxa that

TABLE 1. Community ecology of the insect/arthropod fauna from an old-growth forest: with special emphasis on the canopy fauna. An overview of the site designations and sampling techniques.

	SITE					
METHOD	Canopy	Forest floor	Trans-ition zone	Clear-cut	Second growth 1	Second growth 2
Pan/Window	NO	YES	YES	YES	YES	NO
Malaise	YES	YES	YES	YES	YES	NO
Moss cores	YES	YES	YES	YES	NO	NO
Branch clip	YES	NO	NO	NO	NO	YES
General collect	YES	YES	YES	YES	YES	YES

can be collected by each method, have been summarized by Winchester and Scudder (1993) and the Biological Survey of Canada (1994). The methodologies used in this study at each site are presented in Table 1 and were run for 5 months (June-October) in 1991 and for 7 months (May-November) in 1992. Elaboration of the 1991 sampling design is given below. The 1992 component of this project is in the initial stages of specimen preparation and will not be included in this paper.

Branch Clippings

The branch clipping program was conducted in the five Sitka spruce trees contained in the fixed-access canopy system. The sampling procedure was modified after Schowalter (1989). In each tree three samples were taken at each of three heights (33, 45, and 54 metres). A total of 45 branches were collected for each of six sample periods. Samples were collected in one-month intervals from May-October, 1991. All insects were removed from each sample and prepared for identification. Immature individuals were reared to maturity. Single branches from each tree and level were run through Tullgren funnels to extract Collembola and Acari. After sorting, all branches were dried, and then total branch weight and needle weight were recorded. Various other measurements were taken from the branches but are not relevant to the present analysis and will be reported in later papers.

Malaise Traps

Five Malaise traps (Townes 1962), randomly placed along a linear transect, were run at each of 4 sites (Table 1). Arthropods were collected into 70% ethyl alcohol to which 6 drops of ethylene glycol had been added. Traps were cleared at two-week intervals from May-October. A total of 245 trap samples were collected. Arthropods from each trap were sorted and enumerated. These samples are in the process of being prepared for sending to taxonomic experts for identification.

Window/Pan traps

Five window/pan traps were run at each ground sample site (Table 1). Pans (23 X 15 X 5 cm) were buried with rims flush at ground level. They were randomly placed along a 50 m linear transect. A clear glass window (0.5 by 0.5 m) was placed above each pan trap. A saturated salt solution was used as a preservative with a few drops of detergent added as a wetting agent. A total of 120 trap samples were collected. All arthropods were washed in water and stored in 75% ethyl alcohol. Specimens of the families of interest were then removed and prepared for shipment to taxonomic experts for identification.

Moss Cores

A hand held moss/soil corer (approx. 3 cm X 5 cm) was used to collect 5 moss/soil cores at random from each sample site (Table 1) once a month from May-October. A total of 120 cores were collected. In the laboratory each core was extracted through a Tullgren funnel for forty-eight hours. Samples were preserved in 75% ethyl alcohol. Volume displacement and dry weight were recorded for each core sample.

Results

In total, an estimated 800,000 arthropod individuals were captured during the 1991 sample season. Only a small proportion of these samples (approx.

40,000 individuals) have been identified and from this data set only selected examples will be used in this paper.

An informative view of canopy arthropods can be gained by placing them in guilds. The guilds used in this study are structured after work done by Root (1967, 1973). We recognize six guilds: phytophages, which feed on living plant material; the epiphytic fauna, which live on and are associated with the surface of plants; scavengers; predators; parasitoids and tourists. The tourist guild is composed of those individuals which represent non-resident fauna that are dispersing between habitat types. Further elaboration of these guilds is given by Moran and Southwood, (1982). Guild structure, expressed as mean biomass per kg. of dry plant material for all arthropods from the 1991 branch clipping program (Figure 2), indicates that phytophagous and predator guilds occur in the highest proportions and these proportions are approximately equal.

The data for staphylinid beetle species rank and abundance are plotted in Figure 3. The forest floor and transition zone exhibit a pattern appearing most similar to the log series model (Fisher et al. 1943), while the canopy and clear-cut zones exhibit no apparent patterns when compared to the geometric, log series, log normal or broken stick models. Numerical relationships between staphylinid species and study sites (Figure 4) indicate that the transition zone had the greatest number of species (49) while the canopy had the least number of species (6). The forest interior and transition zone had the most species in common (20) while the number of species shared in common between the forest interior and clear-cut is low

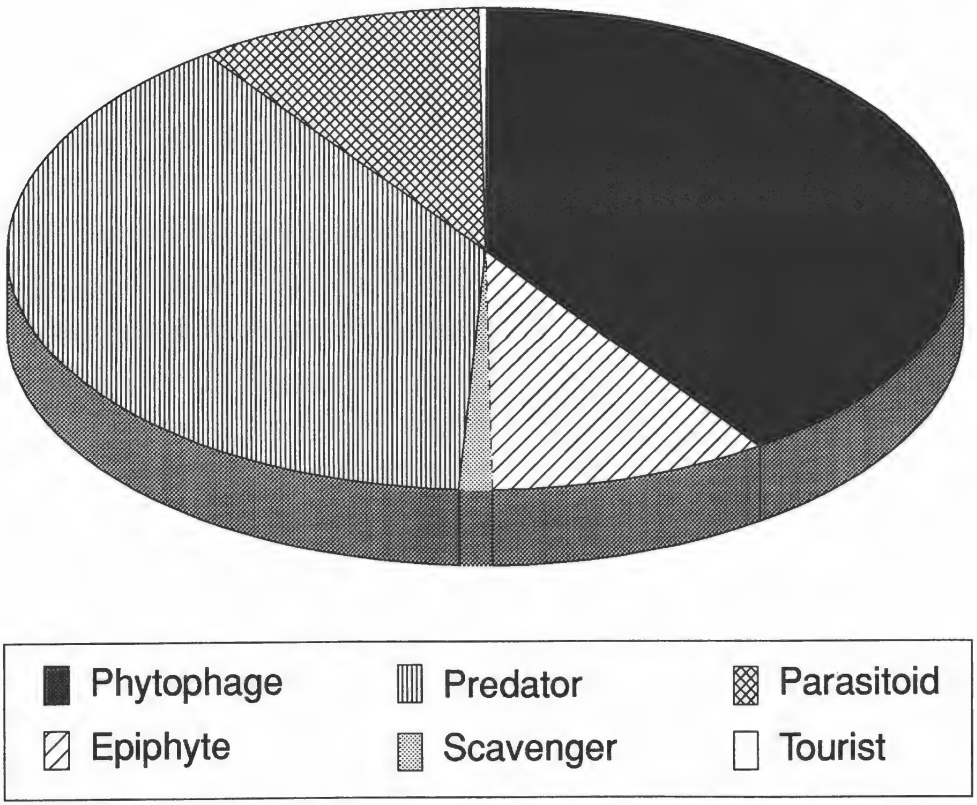

Figure 2. Guild structure of the arthropod fauna from all trees expressed as mean biomass per kg. of dry plant material. All samples are from the branch clipping program.

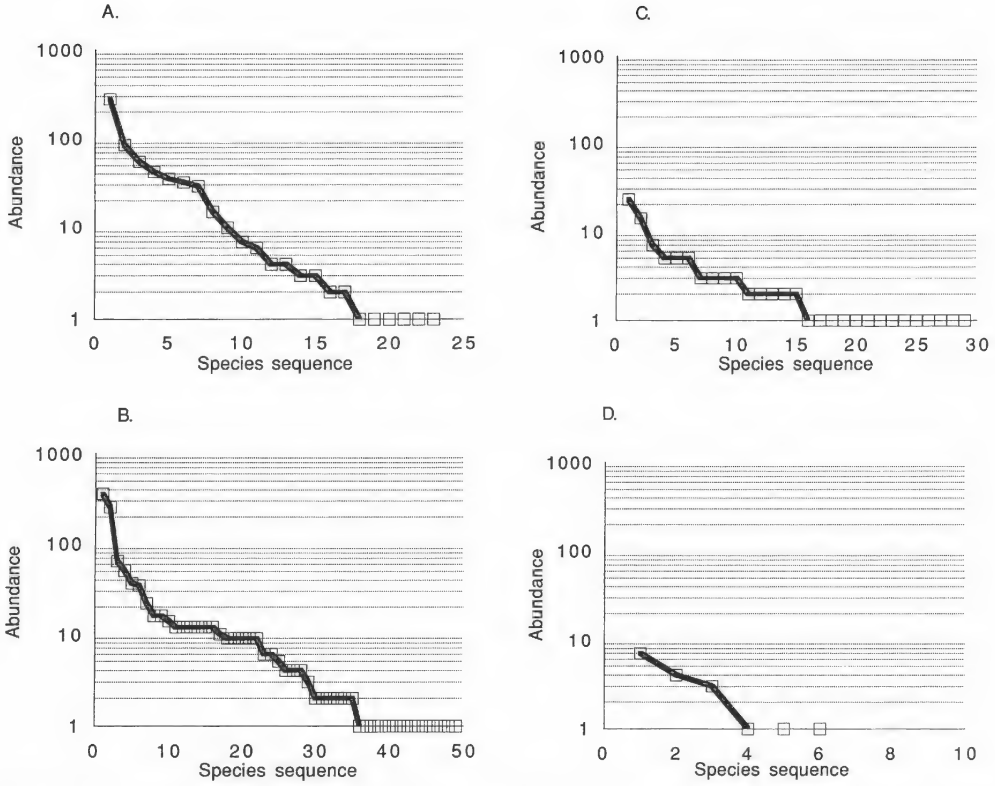

Figure 3. Rank abundance plots of Staphylinid beetles from four sites in the Upper Carmanah Valley. A = Forest floor; B = Transition zone; C = Clear-cut; D = Canopy. Abundance of each species is plotted on a logarithmic scale against the species' rank, the order from the most abundant to least abundant species.

(7). Species turnover, or Beta diversity, between these sites was explored using Jacarrd's coefficient (Table 2). Percent similarity based on species presence/absence indicated that the highest similarity was between the forest floor and transition zone. The clear-cut zone had low similarity when compared to the other sites. The canopy was most dissimilar to all other sites because of the disproportionately low number of species.

Thirty-seven species of spheciform wasp were collected in this study and percentage species similarity using Sorensen's coefficient (Figure 5) indicated that the clearcut and transition zone were the habitats that these wasps preferred. A single specimen was recorded from the forest floor, while no specimens were documented in the canopy. The percentage similarity between the clear-cut and transition zone was 50%. The known prey items of 17 spheciform wasps are listed in Table 3. The prey families of these wasps are most abundant in the clear-cut where they are associated with early successional vegetation. They are least abundant in the forest floor and old-growth canopy zone which lends support to the observed percent similarity between sites.

A subsample of oribatid mites (1000 individuals) were used to look at percent similarity between the canopy and forest floor (Table 4). Even at the family level the canopy oribatids form a distinct assemblage that is only moderately similar to the forest floor oribatids.

Discussion

The general form of the arboreal community is related to characteristics of the tree, and the

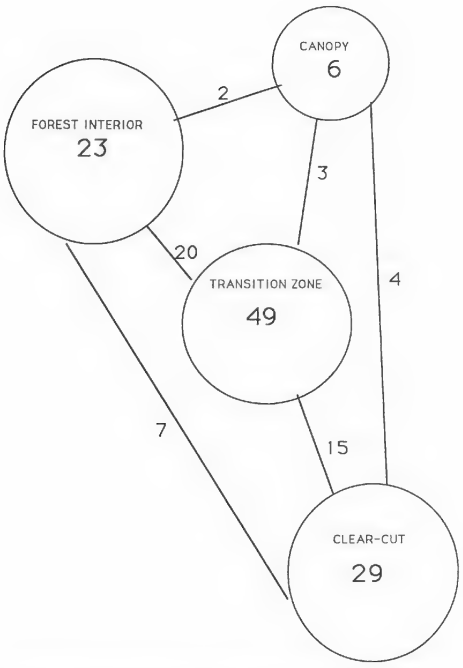

Figure 4. Numerical relationship between staphylinid species in study sites of the Upper Carmanah Valley. Data are pooled from the Malaise and Pan/window trap collections. Numbers along the lines represent those species in common between the sites and numbers within the circles represent those species common to that site.

TABLE 2. Beta diversity (Jaccard's coefficient of similarity) of Staphylinidae caught in Malaise traps from four sites in the Carmanah Valley, British Columbia (temporal sequencing omitted).

	Forest Floor	Trans Zone	Clear cut	Canopy
Forest Floor	1			
Trans. Zone	.65	1		
Clear cut	.12	.20	1	
Canopy	.06	.05	.19	1
# of species	27	39	20	5
# of individuals	486	324	89	24

magnitude of the populations of particular species will be influenced by a variety of factors. The resident canopy arthropod fauna in this study was dominated by the phytophagous and predator/parasitoid guilds, supporting previous studies by Schowalter and Crossley (1987) and Schowalter (1989). Most of the phytophagous guild is composed of species that are feeding on the developing vegetative buds and female cones. These species appear to have a small effect on the host with a negligible loss in developing plant material. We infer from this guild structure that herbivory in this mature, structurally-complex forest is relatively insignificant and, through a series of checks and balances, that large scale herbivore damage (insect outbreaks) is negligible. This information supports previous findings by Reichle et al. (1973), Nielson (1978), Ohmart et al. (1983), and Schowalter (1989) where it was noted that herbivory was less than ten percent of the standing crop in mature forests. The maintenance of a high predator loading in a structurally and functionally diverse ecosystem such as the Carmanah Valley supports previous findings by Kareiva (1983), Risch (1981) and Schowalter (1986,1989).

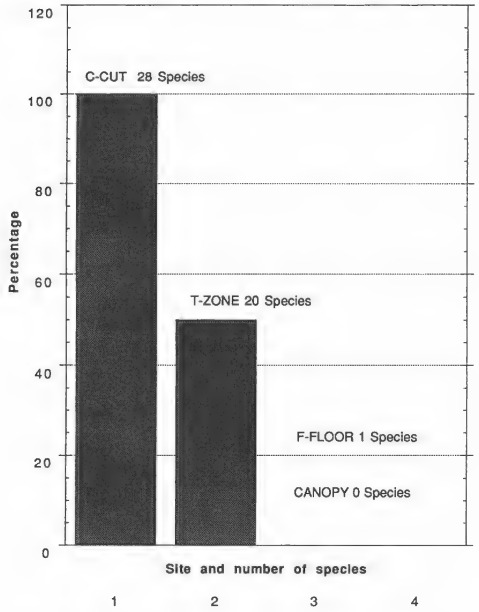

Figure 5. A bar graph comparing the percentage species similarity (Sorensen's Coefficient) of spheciform wasps of the canopy, forezst floor (F-Floor), transition zone (T-Zone) and clear-cut (C-Cut) compared with that of the clear-cut site.

Perhaps the most interesting habitat contained in the Sitka spruce canopy is that provided by the

TABLE 3. List of phytophagous insect prey of spheciform wasps, grouped according to their feeding behaviour.

Prey role	Prey taxon	Predator taxon
Sap feeder	Cercopidae	Pemphredonidae
		Mimesa gregaria
		M. pauper
		M. lutaria
		Mimumesa mixta
		M. nigra
		M. propinqua
	Aphididae	*Pemphredon concolor*
		P. inornata
		Diodontus argentinae
		D. boharti
		Passaloecus armeniacae
		P. monilicornis
		P. patagiatus
		Stigmus inordinatus
		Spilomena sp.
Foliage feeder	Noctuidae	SPHECIDAE
		Podalonia mickeli
	>>Lepidoptera	*Amnophila strenua*

TABLE 4. Comparison of the oribatid ("beetle mite") fauna (subsample of 1000 individuals) from the Sitka spruce canopy and forest floor, Upper Carmanah Valley, British Columbia.

	Canopy	Forest Floor
# of Families	19	21
% similarity = 35%		
# of species	32	36
% similarity = 19%		
# new species	8	15
% similarity = 13%		

4-28 cm deep moss mats which support a well developed soil layer. These mats are primarily composed of four moss species, *Isothecium myosuroides, Antitrichia curtipendula, Dicranum fuscescens* and *Scapania bolanderi* , which are also abundant on the forest floor. Soil microarthopods dominate this canopy soil/litter habitat, a fact which has not been well documented in previous canopy studies. From the small collection of oribatid mites that have been processed to date there is strong evidence that we are dealing with a distinct arboreal assemblage of species. One might expect the taxonomic similarity to be highest between the forest floor and the canopy. However, even at the family level this similarity is low and subsequently is further reduced at finer taxonomic resolution. The discovery of several new species is not surprising given the scope of this study but several of these undescribed species also appear confined to the canopy. We suggest that there maybe enough differences in canopy microhabitat conditions to promote the development of taxonomically discrete species assemblages which in turn would enable these differences to be observed throughout the taxa that comprise the moss mat community.

Habitat changes that occur through logging of old-growth forests have been well documented, but the effect that this type of habitat alteration has on arthropods has only been addressed to a limited extent (McLeod 1980; Chandler 1987,1991; Niemela et al. 1988, 1993; Schowalter 1989; Chandler and Peck 1992). This study indicates that of the 78 species of staphylinid beetles recorded many have not made the transition to the clear-cut site. The majority of the species recorded in the clear-cut are represented by a single individual and it seems unlikely that this indicates long-term habitat use. The canopy habitat does not appear to provide the conditions necessary for this group of beetles, although the one species recorded in any abundance is a new species of Omaliinae which occurs throughout the sampling season. Many of the species recorded in this study are restricted to old-growth forests where two important conditions for survival are met: first, a supply of over-mature, fallen logs which are allowed to decay under natural conditions in the shade of the forest canopy and, secondly, the maintenance of deep layers of undisturbed forest floor litter which have not been eradicated by the extreme conditions of clear-cuts and the subsequent exposure to desiccation and erosion (Campbell and Winchester 1994). Two species, *Pseudohaida rothi* and *Trigonodemus fasciatus* are endemic to British Columbia (Scudder 1994) and specimens of several new species of Omaliinae appear to rely on old-growth forests as a source area to maintain reproductively viable subpopulations.

The depression of species in altered areas such as clear-cuts does not hold true for all arthropod groups. The spheciform wasps from this study

are not a group that inhabits old-growth or canopy areas. These wasps are active fliers and have the ability to seek out prey sources and suitable nest sites for their developing young. The prey base sought by several species in this study are the sap and foliage feeders from homopteran families such as the Cercopidae, Aphididae, as well as caterpillars of the Noctuidae. Members of these families are more speciose and abundant in the clear-cut area where they quickly build up their numbers as they feed on developing seedlings, forbs and shrubs. This accumulation in the phytophagous guild has been well documented by Schowalter (1986, 1989) and Schowalter et al. (1981), a 23-fold increase in aphids followed logging practices has been reported.

Although the analysis of our data is in a preliminary state there are strong trends that indicate that we are dealing with a unique set of organisms that are old-growth dependent. It is not unusual in an entomological study of this scope to find new species. However, several of these species exhibit habitat specificity that restricts their distribution to structural attributes of the old-growth forest both on the forest floor and in the canopy. Forest conversion affects arthropod diversity by altering key patterns of natural processes that are inseparably linked to habitat diversity. The summarizing of these key patterns and documentation of changes due to disturbances should identify ecological roles of arthropods that are at the heart of the biodiversity challenge. The 1.2 million arthropod specimens collected in our study will provide an understanding of the diversity and food web dynamics within these systems, as well as documentation necessary for the elucidation of the biogeographical significance of these species assemblages.

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The International Canopy Network: A Pathway for Interdisciplinary Exchange of Scientific Information on Forest Canopies

Abstract

Forest canopy communities are important in maintaining the diversity, resilience, and functioning of the ecosystems they inhabit. With the increasing interest in and amounts of data on forest canopies resulting from new access techniques, ecologists require tools to manage and analyze their data and to compare data from disparate studies. Canopy ecologists need to deal with new types of data, a great deal more data, and the need to share data among researchers who have separate research questions. With the support of the National Science Foundation, we established an organization to bring together forest canopy researchers, quantitative scientists, and computer scientists to develop methods to collect, store, display, analyze, and interpret three-dimensional spatial data relating to tree crowns and forest canopies. Our activities include compiling the array of research questions and needs from canopy scientists via a survey, examining potentially applicable information models and software tools that are in use in allied fields, and developing conceptual models for the types and format of information and analyses to answer research questions posed by forest canopy researchers. We are also building an interdisciplinary and international communication network (electronic and conventional), organizing the published canopy literature, and serving as a repository for canopy information accessible to scientists, forest managers, and the public.

Introduction

Forest canopy communities are important in maintaining the diversity, resilience, and functioning of the ecosystems they inhabit. In 1993, we created the International Canopy Network (ICAN) to develop methods to visualize, analyze, and understand the complex three-dimensional structure of tree crowns and forest canopies. Our goal in this paper is to explain the impetus for this project and describe our progress toward increasing participation from the forest researcher, manager, and arborist communities.

The forest canopy, which is generally defined as "the aggregate of all crowns in a stand of vegetation, which is the combination of all foliage, twigs, fine branches, epiphytes, as well as the air in a forest" is important for four major reasons. First, the biodiversity within the canopy is exceedingly large, estimated at over 50% of certain ecosystems (Erwin 1983, Gentry and Dodson 1987). Second, the biomass, nutrient and carbon pools, and surface area created by canopy components is large, which can enhance the interception, storage, and circulation of atmospheric nutrients (Carroll 1980). Third, canopy plants provide resources for birds, mammals, and invertebrates within forests (Nadkarni and Matelson 1989). Finally, abiotic characteristics such as windspeed, light intensity, and concentrations of gases within and above a forest are strongly modified by the canopy (e.g., Oke 1987, Fitzjarrald and Moore 1990). Understanding of these organisms and processes would be enhanced by optimizing tools to sample, visualize, and analyze the elements of canopy structure in a statistically rigorous manner.

Historically, canopy studies have been dominated by people seeking the thrill of climbing and following the lure of the discovery of new arboreal species. Recently, the innovation of high-strength and low-cost canopy access equipment has made more detailed canopy study an option for scientific research. With the development of effective technological climbing methods such as the "canopy raft" (Hallé 1990), the canopy crane (Parker et al. 1992), and of ground-based methods such as fogging (Erwin 1983), researchers can now spend less time fretting over how to get into in the treetops and more time analyzing and interpreting canopy data.

Within the last decade, scientific interest in the canopy has burgeoned remarkably (Russell et al. 1989, Lowman and Nadkarni 1996). The number of scientific publications on canopy structure has grown at a disproportionately rapid pace relative to the general field of biology (Fig. 1).

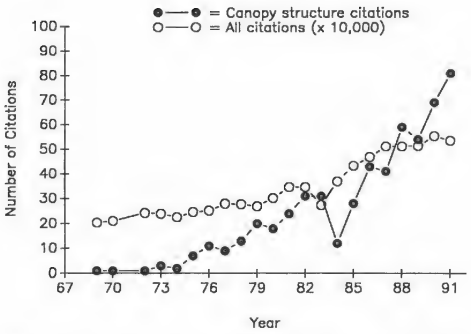

Figure 1. The rate of scientific literature published on canopy structure compared to the rate of literature published in the general biological literature. Data points are the number of citations with keywords related to canopy structure tallied in a bibliographic search of the database BIOSIS (closed circles) and the total number of all citations indexed in BIOSIS for that year (x 10,000) (open circles). Note that the rate of publications about canopy structure greatly exceeds the rate of all citations after 1984, indicating the explosion of interest and study of forest canopy structure in recent years.

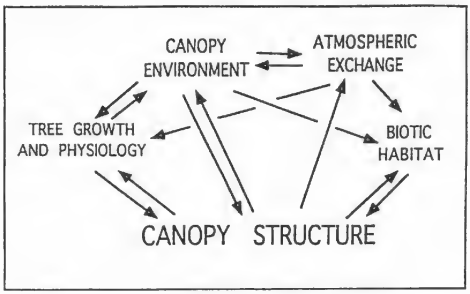

Figure 2. The complex interrelationships of canopy structure among different areas of canopy science.

Aspects of the canopy have been the focus of many recent symposia, scientific books, and popular articles and other public media. This focus is related to increasing concerns over conservation, biodiversity, global atmospheric change, and the management of rain forests.

Tree crowns and forest canopies are spatially complex, three-dimensional structures that are temporally dynamic. Knowledge of canopy structure lends insights into the interrelated fields of biotic habitat, canopy environment and atmospheric exchange and tree growth and physiology (Fig. 2). In a sense, the idea of "structure" sits at the interface between organism and environment, and thus at the heart of ecology itself. "Forest structure" has historically been approached from many standpoints, e.g., from the standpoint of tree architecture (Hallé et al. 1978) or physiological and morphological processes (e.g., Ford 1992). It has meant the organization of the species in a community, often with a ranking by density or bulk (e.g., a histogram giving for each species its foliar biomass) (Parker et al. 1989). Others have drawn stick figures giving the shapes and positions of tree crowns and attendant organisms, using work-intensive techniques of surveying from the ground (Nychka and Nadkarni 1990). Finally, forest ecologists and managers have attempted to measure canopy structural diversity from ground measurements and using remote sensing technology (e.g., Sorrensen-Cothern et al., in press).

Both the types and amounts of canopy structure data are changing rapidly. In the past, the simplicity of rope-climbing generated studies by scientists who worked singly or in small groups and produced fairly small data sets. The ease with which recent access innovations permit multiple teams of scientists to work within the same volume of the canopy, however, results in complex and expensive data sets that must be used jointly. For example, although projects on the canopy crane in Panama started out as largely independent, plans for an upcoming study feature a coordinated effort that involves teams working on complementary projects such as leaf nutrients, leaf allozyme activity, and insect diversity, all in relation to a common database of canopy structure (S. Mulkey, pers. comm.). Similarly, the canopy crane that was erected in the Pacific Northwest, during 1995 on the T.T. Munger Research Natural Area in Washington, will be used by a group of associated scientists who will ask questions on subjects ranging from tree architecture to the effects of air pollution on canopy lichens. These investigations will require spatial information on the underlying substrate (i.e., tree trunks, branches, and foliage), not only for its own sake, but also to relate forest canopy data to allied data sets. Thus, in the near future, canopy scientists will have to deal with new kinds of data, more data, and the need to share data.

Data collected by canopy research teams are likely to be extremely useful to other scientists such as geographers and land use managers, just

as data emanating from allied fields could aid forest canopy researchers. Such "retrospective" use of data, however, requires the foresight to collect and record information that can act as a bridge to integrate separately collected data.

Having ascertained that questions involving the structure of the forest canopy are recognized as important, and that new methods of access are available for data collection, we anticipate an urgent need to deal with the new information on forest canopies that will be forthcoming in the next few years. To date, no one has worked out quantifiable and cost-effective methods to characterize tree crowns and forest canopies. Field ecologists are notorious for their independent (at times idiosyncratic) ways of taking, storing, and analyzing data. In many ways, the current situation is analogous to what planetary scientists faced when anticipating data from space probes: large quantities of new types of data that must be shared by a variety of scientists asking different questions. With the increasing interest in and amounts of data on forest canopies, ecologists require tools to plan for developing the means to collect, process, store, analyze, portray visually, interpret, and distribute these types of data.

With the support of a two-year planning grant of the Database Activities Program of the National Science Foundation, we established an organization to bring together forest canopy researchers, quantitative scientists, and computer scientists to establish methods to collect, store, display, analyze, and interpret three-dimensional spatial data relating to tree crowns and forest canopies. We call this organization the International Canopy Network (ICAN). The interdisciplinary nature of this project requires the interweaving of expertise from three types of participants: "domain scientists," scientists working directly with research related to tree and forest biology such as tree physiologists and ecosystem ecologists; "structural information specialists," scientists who have developed the capability to analyze 3-D structural data in allied and non-allied fields (e.g., hydrologists, astronomers, medical doctors); and "computer scientists," scientists working with questions about information management, storage, and analysis.

Project Activities and Products

Activities for the first two years of the ICAN include five steps (Fig. 3): define ecological questions and needs about canopy structure by canvassing domain scientists; compile lists of existing conceptual and applied approaches, databases, and tools from structural information specialists; develop a preliminary conceptual information model and recommendations for data analyses with input from computer scientists; "test" the feasibility of the preliminary information model and recommendations with a set of pilot field data collected by domain scientists, and if necessary, modify the model and recommendations; and

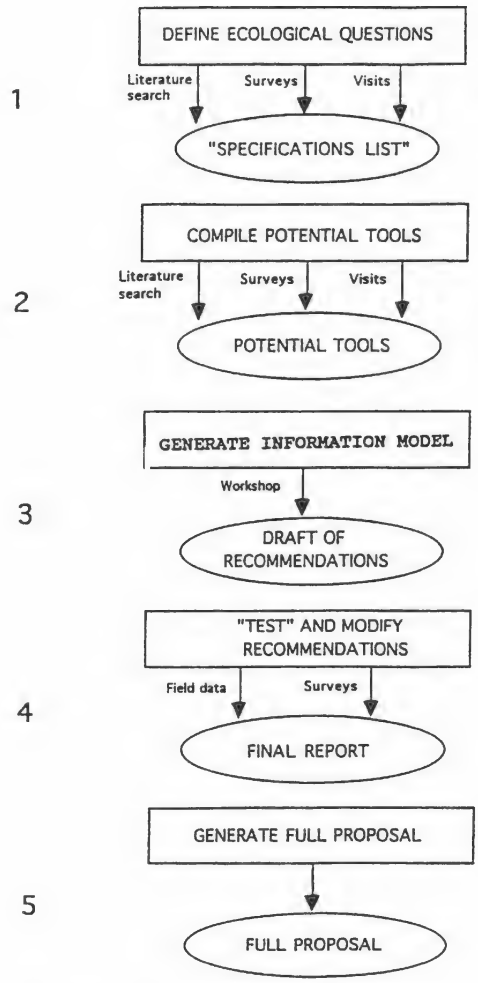

Figure 3. Five research activities and products of the International Canopy Network.

communicate the model and recommendations to the science community and plan for implementing the results of this planning project.

Our first step is to define the questions and needs on canopy structure by canvassing domain scientists. We are surveying the diverse community of canopy scientists to understand the scientific issues that are now believed to require information on canopy structure; the specific attributes of canopy structure for which information is required, and the manipulations and displays now being used. This process consists of three activities: a literature search and summary of books, journals, and existing software; surveys and interviews via telephone, conventional mail, and electronic mail (which have been developed with the help of a consultant sociologist experienced in developing such surveys); and organization of communications pathways among canopy scientists by establishing an electronic mail bulletin board (called "CANOPY"), which is currently administered by the Long-Term Ecological Research (LTER) network office at the University of Washington.

In October 1993, we sent out a four-page survey to 430 domain scientists, compiled from participants in canopy symposia, authors of current papers about canopy structure, and other professional contacts. We are currently summarizing the results of the survey, to which 220 scientists responded. Results will be synthesized into a publication and circulated on the canopy electronic bulletin board. The end product of these steps will be a "specifications list" which will identify issues and questions of concern to forest ecologists, a roster of currently available ways to collect and analyze canopy data, and a list of suggestions for potentially useful models and tools to overcome the perceived obstacles to canopy science.

Second, we will compile the existing approaches and tools from structural information specialists in other fields. We wish to discover if appropriate approaches and tools such as software and statistical tests for working with canopy structure already exist in other fields and need not be re-invented. We are currently identifying existing methods for working with spatial information from researchers in allied and non-allied fields who deal with large amounts of three-dimensional spatial data of tree-like forms. Examples of fields we are investigating include oceanography, electrical engineering, astronomy, hydrology, and medicine (especially tomographic and vascular systems research). We will pursue this process through literature surveys, interviews, and resource visits. We have also placed announcements in scientific journals; 230 announcements were sent to a wide variety of journals, and more than 40 are publishing them.

Third, we wish to develop a preliminary conceptual information model with input from database and computer scientists. This model will be adaptable to multiple applications and implementation must be affordable. Our method will be to invite a panel of database and computer scientists (8-10 individuals) to work with us. Participants will be identified through contacts we make during our surveys. Individuals on this panel will be sent the specifications list from domain scientists and the "potential tools" list from structural information specialists (Fig. 3). At their home institutions, they will individually work on creative solutions.

At the beginning of the second year (1995), we will convene a three-day workshop at The Evergreen State College to facilitate discussions. At the beginning of the workshop, the research to date will be reviewed. Particular software and other "products" will be demonstrated. This will be followed by brainstorming sessions. After the workshop, participants will submit a written report of their ideas, which will be included in the draft report of recommendations. Using information modeling methodology, we will develop an information model that integrates data and data analysis requirements.

Our fourth step is to examine the feasibility of the recommendations with a set of pilot field data collected by domain scientists. To learn whether the types and amounts of data called for in the recommendations are realistic, we will collect a set of pilot data at a field site where the canopy is accessible. This stage functions as a feasibility study, to determine whether the types and size of data required by potential models are practical, i.e., whether field researchers can collect the required data within a realistic schedule and financial budget. Depending on our progress, we may also be able to use these data to try out candidate analytical database packages, i.e., to create a visualization of a real forest canopy. With the actual measurements, we will know what degree of

accuracy, repeatability, intensity of effort, and cost the various data management strategies will require.

We anticipate that a set of pilot data will be collected at the field site of the canopy crane in the Pacific Northwest. For example, the heights and angles to a series of points on branches recorded from a central benchmark might be useful to construct a three-dimensional map of the canopy. Maneuvering the mobile boom of the canopy crane would allow these data to be taken safely and relatively easily. If necessary, the recommendations will be modified, based on the field experience and feedback from participants.

The fifth step is to generate a strategy for implementing our recommendations for this planning project, which may include a major proposal to the National Science Foundation and other agencies. Our objective for this final stage is to ensure that the information model developed can be implemented and made available for use to forest canopy and spatial information specialists.

Future Directions

Although we recognize that forming a scientific communication network cannot replace independent scientific projects as the true "stepping stones" of academic inquiry about canopies—these complex and important pieces of our landscape, we believe that facilitating communications, forging avenues for multidisciplinary exchange of ideas, and putting people, equipment, approaches, and databanks together in innovative and creative ways can enhance our understanding of forest canopies. As with other established scientific networks (e.g., the LTER, supported by the National Science Foundation), productive intersite and interdisciplinary insights can be expected from these activities.

Our major hope is that this process will result in free-flowing exchange of information and concepts among those addressing canopy questions from various approaches. For example, quantifying canopy structure will allow those studying canopy-atmosphere interaction to better relate their data to those viewing the canopy as habitat for biota, and for those studying tree crown growth and physiology (Fig. 2). We hope for strong and active participation from other forest scientists, resource managers, and computer specialists. We are excited at the interdisciplinary nature of the task, and at the communications pathways we are forging both within the field of forest ecology and outside our disciplines. Most important, we are enthusiastic about taking steps that will provide greater ease and more understanding about the complex structure of forest canopies.

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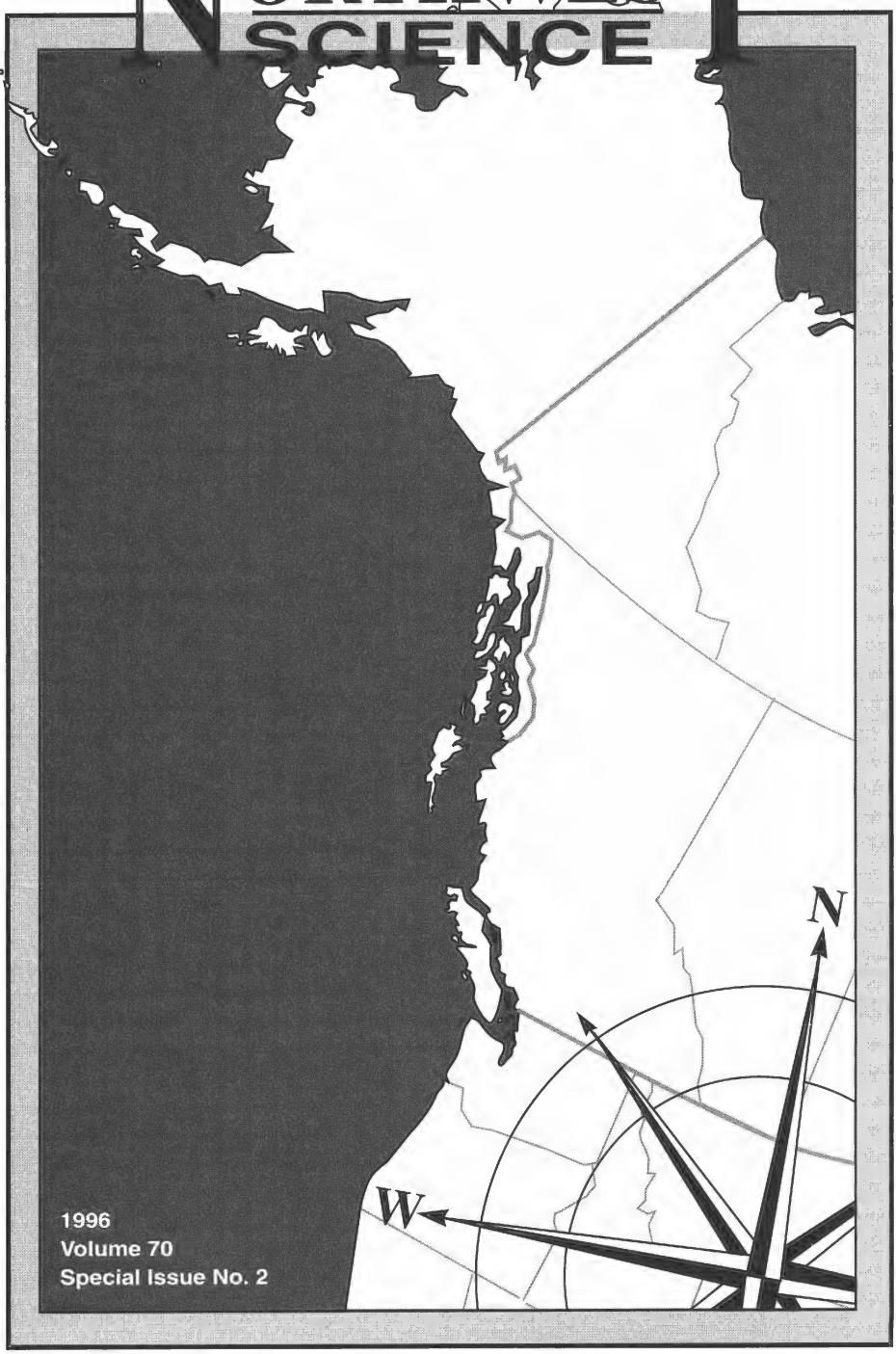

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Editor's Note

The aquatic resources of the state of Oregon are diverse, including a wide range of lakes, rivers, and coastal systems. Its lakes have attracted considerable scientific interest during the past two decades, partly because of their intrinsic value as natural systems and partly because of concern that humans may be altering their chemical and physical properties. Until the last hundred years or so, human populations had minimal impacts on most of the lakes of Oregon. However, the ecological integrity of some lakes is potentially threatened by human settlements, forest harvest practices, and various uses of hydrological resources. A better understanding of the function of lake ecosystems will provide the context for monitoring potential changes in water quality and for protecting aquatic systems. This special issue of *Northwest Science* investigates the aquatic ecology of Oregon lakes, and emphasizes the need for integrating scientific information in future management decisions that may affect them.

For additional copies of this special issue, contact the Guest Editor. For reprints of individual articles, contact the senior author of each article.

Preface

The articles in this issue reflect a collaborative effort by members of the Oregon Lakes Association. The Oregon Lakes Association is a non-profit organization whose primary purposes are to promote understanding, protection and thoughtful management of lake and watershed ecosystems in Oregon. This issue includes articles about six Oregon lakes, along with an overview of these articles, and description of the lakes in the various ecoregions of the state.

Publication expenses for this issue have been provided by the Pacific Northwest Ecoregion Program of the U.S. Environmental Protection Agency, the Biological Research Division of the U.S. Geological Survey, PacifiCorp, and the Oregon Lakes Association. We appreciate the contributions of these supporters, and the assistance they have provided to help promote understanding and protection of the lakes of Oregon.

As editor of this issue, I have greatly appreciated the authors' enthusiasm and hard work, and their patience in waiting for the completion of all articles so they could appear together. It is my hope that this issue will be useful to both scientists and resource managers in the Pacific Northwest and elsewhere. I also hope that this will be followed with future publication of additional studies on Oregon's lakes.

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Scientific and Management Issues in Oregon's Lake Ecoregions

Abstract

In this overview paper we describe the ecoregions of Oregon, briefly characterize the lakes in each region, and summarize the lake management problems of coastal and Cascade lakes, two ecoregions represented in this issue. Shallow coastal lakes are often naturally mesotrophic or eutrophic, and thus support profuse populations of aquatic plants. Four coastal lakes reported on here, Devils, Woahink, Mercer, and Munsel Lake, represent a range of depth and trophic levels; all currently experience high development pressure. In contrast Cascade lakes are more often located in protected areas of federal land and in wilderness areas, and thus experience more pressure from recreational than from residential use. In this overview, we present three studies of contrasting lakes in the Cascade ecoregion: (1) a protected lake of renown, Crater Lake in Crater Lake National Park, (2) one of the world's most dilute lakes, Lake Notasha, located in a wilderness area, and (3) a more impacted power-generating reservoir, Lemolo Lake. Finally, we applied a cluster analysis on lake chemistry variables and compared the geographic distribution of clusters to ecoregion boundaries. In general, we found a geographic distribution to the identified clusters that paralleled ecoregion boundaries. The ecoregions provide useful background for widescale management decisions.

Introduction

It has been hypothesized that ecosystem quality is determined by natural and anthropogenic factors that interact in space and time, and thus can be described geographically. Attempts to delineate ecological regions in the United States for the purpose of assessing ecological integrity have included the major land resource areas (MLRA, Austin 1972; USDA 1981), ecoregions of the United States (Bailey 1976), potential natural vegetation (Küchler 1970), and Omernik's ecoregion of the coterminous United States (Omernik 1987). Omernik's approach has been widely used in recent years for providing a framework for environmental management (Gallant et al. 1989; Omernik 1995), and for assessing surface water quality issues (Hughes and Larsen 1988).

The Omernik (1987) approach for defining ecoregions is based on the hypothesis that ecosystems and their components display regional patterns that are reflected in spatially variable combinations of causal factors, such as climate, geology, soils, vegetation and physiography. Omernik's compilation for the coterminous United States (scale 1:7,500,000), was based primarily on qualitative assessment of four data sources: major land uses (Anderson 1970), classes of land-surface form (Hammond 1970), potential natural vegetation (Küchler 1970), and soils maps from various sources. In addition, Omernik selectively used maps of surficial geology (Hunt 1979), physical division (Fenneman 1946), land resource regions and major land resource areas (USDA 1981), and climatic maps (Baldwin 1973), in deriving subjective regional delineations. Omernik and Gallant (1988) also noted that forest type and stream density have been useful in delineating ecoregions. Boundary delineation was based on expert judgement and the degree of spatial overlap of the component maps. Gallant et al. (1989) recognized that, in some areas, the designated ecoregions were too heterogeneous to be of great use for management purposes. They therefore advocated partitioning regions into subregions, where necessary, using a similar method, but with higher resolution data sources.

As the introductory and overview paper for this special issue on Oregon lakes, this paper: (1) describes the lakes located within Oregon's ecoregions, and (2) presents some of the management issues in these regions, especially as they have been identified in the companion articles of this issue. Eight major ecoregions in Oregon have been described by Clarke et al. (1991) and by Omernik and Gallant (1986). In this paper, we provide a description of the lakes in each ecoregion, and summarize some of the lake management concerns in each ecoregion. Finally, we will compare the results of a cluster analysis performed

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on lake chemistry variables, with the geographically derived ecoregions, to demonstrate how well the ecoregions predict lake chemistry.

The papers in this issue present detailed limnology of lakes in the Coast Range and Cascade ecoregions. The main objective of these companion articles has been to present detailed limnological studies covering several topics. The wide variety of lakes within these regions is represented in the companion articles that describe lakes from oligotrophic to eutrophic, large to small, and located in wilderness and urban areas.

Ecoregions of Oregon

Oregon's ecoregions have been delineated by Omernik and Gallant (1986), and refined for water quality management by Clarke et al. (1991). For the comparisons in this paper, we have used the classification by Clarke et al. (1991), because it is being used by state agencies in Oregon, both the Division of State Lands, and the Department of Environmental Quality, for organizing land and surface water management activities. The 2303 lakes of Oregon, Clarke's ecoregions, and the lakes described in the other articles of this issue are presented in Figure 1.

In order to describe the lakes of each ecoregion, we needed data for many lakes across each ecoregion. This issue includes studies of four coastal and three Cascade lakes. While the detail of these studies portrays important characteristics of lakes in two ecoregions, the numbers of lakes for which we have data is not sufficient to make ecoregion-wide conclusions about the level of heterogeneity within an ecoregion. Several sources of data exist for Oregon's lakes (Johnson et al. 1985; McHugh 1972; Kavanaugh 1973; Larson 1974; Sanderson et al. 1973; Blair and Nelson 1993; Shulters 1974, 1975 and 1976; Rinella 1977 and 1979; Eilers and Bernert 1990; Baker et al. 1968; Campbell 1940; Koski 1957; Stout et al. 1961; Coleman 1953; Hilliker 1959; Multezos 1955; Ziesenhenne 1937; Nelson and Delwiche 1983). Sampling seasons and analytical laboratories differ among the studies, and sampling dates among the studies span decades. Thus,

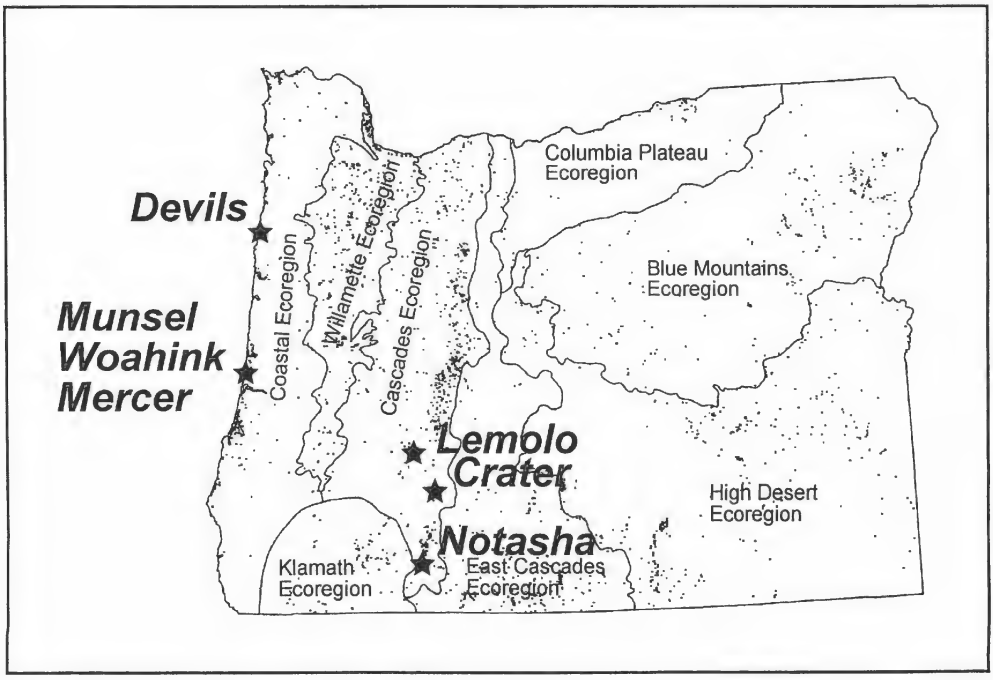

Figure 1. The ecoregions, the 2303 lakes of Oregon, and the seven study lakes included in this issue.

we do not combine data from several studies, but limit the data to the chemical and physical data from Johnson et al. (1985) to capture the diversity of lakes across all eight ecoregions.

The data generated by Johnson et al.(1985) provide good coverage of the state; coverage of each ecoregion varies from 4% to 17% of the number of lakes derived from the 1:100,000 digital line maps described by Eilers & Bernert 1992 (Table 1). The number of Johnson et al.'s lakes within the Coast Range and Cascade ecoregions, is 17% and 12%, respectively. All of the study lakes described in this issue, with the exception of a small Cascade lake, Notasha (Eilers et al. 1996a) were included in Johnson et al. (1985), so to ease comparisons, the data presented in the Tables of this article originate from Johnson et al. (1985). From this table, it is also clear that in every ecoregion, the Johnson et al. (1985) study was biased toward larger lakes. Hence, some of the generalizations made here concerning water chemistry, and lake depth among the regions may not apply to the entire lake population.

The Coast Range Ecoregion

The Coast Range Ecoregion encompasses the coastal lowlands and mountainous areas on the Oregon coast. The land cover is forested with some agriculture and urban land in the lowlands. The majority of lakes are on the 1.5 kilometer-wide coastal strip which extends along the length of the coast. These lakes were formed by migrating coastal sands, by rises in sea level that have closed off streams from the ocean, and by interdunal movements (Smith and Greenup 1939). Lakes in the mountainous area are largely reservoirs

TABLE 1. Numbers of lakes, and means for density, surface areas, and maximum and mean depths for each ecoregion, and values for each lake included in this issue. Values for number, density and surface areas are from digital line graphs (DLG). Data for numbers of lakes and average surface area of lakes included in Johnson, et al. 1985, are in parentheses. Mean and maximum depth are from Johnson et al, (1985), except Lake Notasha (Eilers et al. 1996b). Statistics for ecoregions are in bold print.

Lake	# of Lakes DLG (# in Johnson et al.)	Lake Density per 100 sq km	Surface Area ha DLG (ha. in Johnson et al.)	% in Johnson et al. (1985)	Max. Depth m	Mean Depth m
Coastal	**208**	**0.76**	**29.3**	**17**	**11.2**	**5.1**
	(35)		**(158)**			
Devils Lake			274		6.7	3.0
Mercer Lake			143		11.6	7.1
Munsel Lake			44.5		21.6	9.3
Woahink Lake			331.9		20.7	9.9
Willamette	**390**	**2.5**	**22.7**	**4**	**15.2**	**6.0**
	(14)		**(548)**			
Cascades	**591**	**2.1**	**49.8**	**12**	**43**	**18**
	(71)		**(393)**			
Crater Lake			5371		589	329
Lemolo Reservoir			182		30.5	9.0
Notasha			2.7		10.3	3.5
East Cascades	**294**	**1.1**	**168.2**	**11**	**16**	**6.8**
	(31)		**(1409)**			
Klamath	**87**	**0.82**	**11.2**	**6**	**54**	**16**
	(5)		**(452)**			
Columbia Plateau	**62**	**0.33**	**53.9**	**6**	**58**	**18**
	(4)		**(747)**			
Blue Mountains	**233**	**0.42**	**25**	**10**	**21**	**9.0**
	(23)		**(175)**			
High Desert	**438**	**0.65**	**149.3**	**5**	**13**	**6.0**
	(20)		**(5622)**			

(Ollala,the former Valsetz Lake), or were formed by mass wasting, such as the landslide that created Triangle Lake (Baldwin 1976). Larger lakes such as Devils Lake and Woahink lakes (see Dagget et al. 1996; Eilers et al. 1996a) were formed by sand and beach deposits that blocked the lower portions of coastal valleys.

Coastal lakes are moderate in size, with an average surface area of 30 hectares. Of those lakes sampled by Johnson et al., (1985), the average values for maximum and mean lake depths were 11 and 5 m, (Table 1). Chemistry of coastal lakes in general is moderate (Table 2). Mean pH values reported by Johnson et al., (1985) was near neutral, and conductivity was about 100 µS/cm. The chemical characteristic of coastal lakes that stands out is their high salt content, with above average concentrations of both Na and Cl. This may be due to inputs from ocean aerosols that are deposited in the coastal region increasing Na and Cl in surface water concentrations or from seasonal saline intrusions as documented in a small coastal lake (Lytle Lake, Eilers and Bernert 1995).

Four coastal lakes are discussed in this issue, Devils Lake, Mercer Lake, Munsel Lake, and Woahink Lake. These lakes are located within two kilometers of the coast, and were formed as a result of dunal deposits at the mouths of creeks,

TABLE 2. Mean chemical characteristics of ecoregions, individual lakes, and lake clusters. Data for Notasha Lake from Eilers et al., (1996b), all other data from Johnson, et al. (1985). Clusters were derived from Ca, Mg, Na, K, Cl, and SO_4 data from Johnson et al., (1985), standard deviation of mean cluster values are in parentheses, number in cluster is below cluster title. Statistics for ecoregions are in bold print.

Ecoregion, Lake, or Cluster	pH	Conductivity µS/cm	Alkalinity µeq/l	No_3 mg/L	Total P mg/L	Cl µeq/l	SO_4 µeq/l	Ca µeq/l	Mg µeq/l	Na µeq/l	K µeq/l
Coastal	**7.4**	**106**	**289**	**0.07**	**0.03**	**963**	**66**	**160**	**195**	**587**	**30**
Devils Lake	8.9	105	480		0.03	440	67	235	295	461	8
Mercer Lake	8.7	68	120		0.03	260	56	150	115	318	20
Munsel Lake	7.1	58	120		0.01	358	31	10	123	318	18
Woahink Lake	7.5	60	100		0.04	361	44	105	99	335	15
Willamette	**7.7**	**112**	**746**	**0.12**	**0.03**	**436**	**78**	**380**	**222**	**339**	**28**
Cascades	**7.3**	**29**	**209**	**0.02**	**0.03**	**32**	**17**	**134**	**77**	**85**	**13**
Crater Lake	7.2	108	800		0.17	254	258	464	222	479	46
Lemolo	9.5	47	420	0.02	0.03	39	10	165	115	144	28
Notasha	6.0	3	11	<0.02		5	2.2	7	7	4	2
East Cascades	**8.0**	**108**	**905**	**0.03**	**0.08**	**55**	**208**	**373**	**372**	**367**	**45**
Klamath	**8.0**	**114**	**1084**	**0.02**	**0.02**	**43**	**68**	**590**	**412**	**179**	**24**
Columbia Plateau	**8.8**	**134**	**1155**	**0.04**	**0.10**	**80**	**114**	**516**	**444**	**432**	**63**
Blue Mountains	**7.9**	**80**	**744**	**0.02**	**0.04**	**32**	**61**	**395**	**231**	**201**	**29**
High Desert	**8.3**	**2926**	**18,190**	**0.05**	**0.61**	**82,202**	**714**	**712**	**504**	**34,718**	**951**
Clusters:											
Coastal (38)	7.4	111	359	0.03	0.03	929 (1590)	73 (76)	203 (134)	203 (142)	570 (703)	30 (29)
Dilute (29)	6.9	9	40	0.02	0.43	23 (21)	5 (4)	50 (27)	21 (13)	26 (14)	5 (3)
Moderate (84)	7.7	47	384	0.06		29 (18)	16 (23)	218 (133)	142 (101)	125 (66)	21 (11)
Hardwater (42)	8.2	183	1548	0.07	0.15	97 (89)	291 (536)	730 (477)	569 (529)	616 (567)	79 (55)
Saline (4)	9.6	13,837	80,395	0.21	1.94	410,602 (666,243)	2644 (2086)	267 (153)	261 (210)	170,726 (240,651)	4324 (5192)

combined with fluctuating water levels from melting Pleistocene glaciers (Johnson, et al. 1985). Three of these lakes are considerably larger than the average surface area for the coastal region (see Table 1).

The Cascade Ecoregion

This montane ecoregion is mostly forested. Lakes occur in low density in the western cascades, are primarily reservoirs, and moderate to large in surface area, such as Lemolo Lake (Bonoff et al 1996). The lakes in the eastern, higher altitude area of this ecoregion occur very densely, with over 5 lakes per 100 square kilometers, and are variable in size, ranging from <1 to over 775 hectares. The largest concentration of lakes is in the Central Cascades, from the vicinity of Mount Jefferson south to Mount Thielsen. Most of these lakes were formed by mountain glacial activity, such as Notasha, (Eilers 1996b), although several were created by volcanic activity such as lava blocking stream channels or filling of volcanic craters (Crater Lake; Larson 1996).

Large lakes in the Cascade region tend to be deep, reflecting their glacial and volcanic origins; the lakes sampled by Johnson et al., (1985) have an average maximum depth of 43 m (Table 1). This high average also reflects the bias of the sample toward large lakes. Indeed, the statistically based sample of the Western Lakes Survey (Landers, et al. 1987) estimated average lake size of the 443 Cascade lakes was 3.4 hectares, and average maximum-lake-depth of 4.8 m. The chemistry of the Cascade lakes is somewhat remarkable; these are very softwater lakes, with average conductivity of 29 µS/cm (Johnson et al 1985), and 11 µeq/l from Landers et al. (1987), reflecting extremely low concentrations of major ions.

Three of the lakes discussed in this issue are located in the Cascades ecoregion: Crater Lake, Lake Notasha and Lemolo Reservoir. Lake Notasha and Crater Lake are considered seepage lakes, because they have no surface water inlets or outlets. Both are in protected watersheds, where there is strict control over watershed activities; Lake Notasha is located in the Sky Lakes Wilderness Area, managed by the Winema National Forest, and Crater Lake is surrounded by Crater Lake National Park. Lemolo Lake was formed by the construction of a hydropower dam. It is surrounded by the Umpqua National Forest, but the level of protection in this area is much less than the other two lakes described here. Crater and Notasha Lakes are clearwater oligotrophic lakes, while Lemolo Reservoir is eutrophic, experiencing occasional summer algal blooms and inflated pH. Table 2 with data from Johnson et al. (1985), lists pH from Lemolo Lake as 9.5; data from Bonoff et al. (1996) indicate that such blooms and high pH occur sporadically, and that Lemolo Lake more commonly has pH values of 7.9.

The Willamette Ecoregion

Including the Willamette Valley lowlands and portions of the Umpqua Valley, in the Willamette ecoregion land use is mostly agricultural, interspersed with forested and urban areas. This region has the second largest number of lakes; with the highest density predominantly near major streams and tributaries. Near Portland, close to the Columbia River, a high density of naturally formed floodplain lakes are present (e.g., Sturgeon Lake). Willamette Ecoregion lakes are generally small and shallow (Table 1), related to their origins as oxbow and constructed lakes. The somewhat high alkalinity values (Table 2) are associated with the high base cation concentrations, and reflect a geology of softer, more easily eroded materials. The high nitrate levels (Table 2) observed in these systems may also reflect the extensive disturbed land in the region, both of an urban and agricultural nature. Lakes in this region have been extensively studied by several investigators (Rinella et al. 1977 and 1979; Shulters 1974, 1975, and 1976; Sanderson et al. 1973).

The Klamath Mountains

The Klamath Mountain Ecoregion is forested in upper locales where lakes are scarce, but in the lower valleys lakes are more common. The greatest concentration of lakes is east of Medford in the Rogue Valley. While the density of lakes in this ecoregion is not unlike that of the coastal ecoregion, lakes in this region are considerably smaller (Table 1). Alkalinities and pH here are high (1084 µeq/l, 8.0, respectively; Table 2), and are associated with high Ca (590 µeq/l).

The East Cascades Ecoregion

Characterized by a mixture of forest land, agricultural land and steppe, lakes are uncommon in the East Cascades except in the lake basin near

Klamath Falls. The National Wildlife Refuge near Upper Klamath Lake is home to a large population of winter waterfowl. Many small marshes and seasonal lakes also occur in the East Cascade ecoregion. Although most lakes in this region are small, this ecoregion has the largest average lake size (168 ha), due to the inclusion of Klamath Lake, with the largest surface (941,500 ha) area of any of the Oregon lakes. Chemistry here is typical of lakes east of the Cascade range; somewhat alkaline pH, and moderately high alkalinity, and again high Ca (8.0, 905 µeq/l, 373 µeq/l respectively; Table 2).

The Columbia Plateau

Lakes are uncommon on the Columbia Plateau region of steppe interspersed with agricultural land. This area has the lowest number (62) and density (0.33 lakes per 100 sq km) of lakes (Table 1). Small irrigation and farm ponds in the Hermiston area are common; the tablelands & dissected uplands have virtually no lakes. Average lake size in this ecoregion is moderately large (Table 1). These lakes have similar alkalinity to those in the East Cascade and Klamath regions, but with a somewhat higher average pH (8.8). It is not clear if the observed higher pH reflects a greater incidence of eutrophication in this region, or results from geological inputs.

The Blue Mountains

Lakes are located in alpine and subalpine areas of this rugged mountain landscape. The Wallowa and Blue Mountains have the highest density of lakes, typically moderate to small in size. These lakes were mostly formed by glacial activities. While many are alpine, the chemistry of the lakes sampled by Johnson et al. (1985), is more reflective of the harder water, lower elevation lakes in eastern Oregon. Average alkalinity of the lakes sampled by Johnson et al. (1985) is 744 µeq/l, pH is 7.9, and conductivity is 80 µS/cm. These average characteristics reflect a sample of lakes that include the larger lakes in the region (Table 1). Due to the inclusion of more large lakes in the sample, the average chemistries reported here may not accurately represent the average chemistry of the ecoregion. Lakes in the alpine area of this region sampled in the Western Lake Survey (Landers et al. 1987), had a median conductivity of 13 µS/cm, reflecting the dilute nature of these high elevation lakes.

The High Desert

Not surprising given its name and arid character, the High Desert Region has a low density of lakes, with the largest concentration in the Warner Valley. Land use here includes forest, range land, agriculture and barren land. Many of the lakes are seasonal due to varying climatic regimes, and were formed by tectonic uplifts, faults and tilting (such as Abert Lake). These lakes tend to be very large and shallow (Table 1), and include Oregon's saline systems, as reflected in the region's chemistry (Table 2). Extreme values of conductivity (2926 µS/cm) result from the very high concentrations of Na and Cl (34,714 µeq/l and 82,202 µeq/l, respectively).

Management Issues

Coastal Lakes

In general, coastal lakes appear to be affected by three problems: increased eutrophication, increased sedimentation rates, and lush growth of introduced aquatic macrophytes. Increased sedimentation rates can effect lake water quality in several ways. Decreased lake volume will result from the increased load of sediment deposited near inlets as stream flows decrease entering the lake. Phosphorus (P) attaches to soil particles, and is carried into lakes with erosional materials. Once in the sediment of the lake, the P may be released to the water column, supporting algae and macrophyte growth. High sediment loads often cause increased water turbidity and decreased water clarity. Lush macrophyte growth slows water movement, increasing sedimentation rates, but also improving water clarity. Management strategies that reduce these problems include decreasing erosion from upstream sources, and decreasing the amounts of nutrients applied as fertilizers (or otherwise entering the water) around and upstream of the lake. These pollution sources are often difficult to control because of their non-point source distribution. Small inputs may not appear sufficient to cause problems, but several small sources throughout a watershed will result in water quality problems.

Recent activities that have accelerated erosion over the last 30 to 50 years prevail along the entire coastal zone, affecting all of Oregon's coastal lakes. Forest logging and residential development account for most of the problems, although

agricultural sources including animal grazing occur in some areas of the coastal zone as well. Recent and planned rule changes such as the Forest Practices Act (OAR 1994) and the Coastal Zone Management Non Point Source Management Plan (CZARA 1990) address erosion problems. Unfortunately, while decreasing nutrient inputs will address long-term eutrophication, large stores of P in lake sediments remain accessible to lake flora, so observable effects of control programs on lake water quality may not be realized for many years.

Although over-growth of aquatic macrophytes create undesirable problems, absence of macrophytes may be worse. Aquatic macrophytes increase water clarity by decreasing water flow, and allowing suspended particles to settle. They also discourage erosion from lakeshore areas, thus decreasing shoreline erosion and sediment loads from in-lake sources, especially in lakes susceptible to wind-driven mixing. Communities of native species are regulated by predators and disease, while invasive, non-native populations, lacking these local controls, grow in extreme abundance. This abundant growth can increase water column pH, and cause large swings in dissolved oxygen, reducing water quality for other aquatic organisms. Eradication of macrophytes, however, encourages algal blooms and high turbidity, which often create bigger impairments to lake use, and can be aesthetically less desirable. Management objectives should thus strive to limit, but not eliminate macrophyte growth.

Of the four coastal lakes discussed in this issue, Devils Lake is both the most shallow and most influenced by urbanization. Not surprisingly, it has had severe macrophyte problems as well. Recently the lake has been the subject of a series of Clean Lake Studies (KCM 1983; Anon. 1994) and the site of an experimental introduction of grass carp (*Ctenopharyngodon idella*) to control the macrophytes. While the carp have successfully lowered the macrophyte population, this in turn has led to increased turbidity and algal blooms, so water quality problems associated with high pH and low dissolved oxygen are still common (Wagner, pers. comm). The diatom flora in a sediment core of Devils Lake indicates that little change in the species assemblage has occurred for the past 150 years, suggesting that the lake was eutrophic before the increased development pressures of the last 30 years. Data from this core also showed that sedimentation rates increased concurrent with European settlement in the area. The rate of sediment accumulation has accelerated in the last thirty years, a time when housing construction increased around the lake and within the watershed. Current activities are addressing areas of high erosion through stabilization and vegetation remediation.

Mercer Lake has experienced degraded water quality with increased population and recreational use (Bryant 1979). Mercer Lake is mesotrophic, bordering on eutrophy; Munsel and Woahink Lakes are classified as slightly mesotrophic and oligotrophic respectively (Daggett et al. 1996). The work reported on here by Daggett et al, suggests that a similar future of increased eutrophication awaits Munsel and Woahink Lakes. Unfortunately, extensive management activities, similar to those taking place on Devils Lake, have not yet begun on these lakes.

Cascade Lakes

The two most common management issues in the Cascade Ecoregion are sedimentation and eutrophication. This region is not heavily developed, so forest activities and erosion from roads account for most of the sediment sources. As described above, eutrophication accompanies sediment delivery. Eutrophication can also be a problem in areas with high recreational activity, especially in remote areas with limited sanitary facilities, for example, Crater Lake, and Lake Notasha, described in this issue, along with many others across the state. Decreases in water clarity over the past decade prompted the National Park Service to disconnect the septic system serving the Crater Lake Visitor Center, and divert the sewage to a treatment pond outside of the crater, although study results later indicated that the observed change in clarity was due to natural causes (Larson 1996).

Lake protection in wilderness areas should include shoreline and riparian vegetation, and trail maintenance and protection, which in turn will protect hydrologic pathways to lakes Eilers et al. (1996b). Protection of hydrologic pathways to dilute lakes, in particular, is important, because their chemistry results from the balance of water from several sources, and could change dramatically with a change in water source. These activities alone may not fully protect alpine lakes. Natural sources of P occur throughout the Cascade region. These may account for the highly

eutrophic state of Lemolo Reservoir as there is not heavy agriculture or sources of fertilizer associated with human habitation. Although it is downstream of Diamond Lake, a heavily used, eutrophic system, Lemolo receives a relatively small portion of its water from this lake. Despite the high use that Diamond Lake receives, nutrients are thought to occur naturally at high levels (Lauer, et al. 1979). If so, this may be true throughout the Lemolo watershed. This lake then, may be naturally eutrophic, so that management activities may succeed only in reducing further degradation of the high pH, dense algal blooms, and high biological oxygen demand currently present in the lake.

Lake Classification by Cluster Analysis of Chemical Attributes

We were interested in comparing the distribution of lakes with similar chemistry, to their distribution across ecoregions, in order to assess how well the ecoregions predict water quality characteristics. In order to do this, cluster analysis on the lake data from Johnson et al. (1985) was used to group lakes into unique clusters based on ionic chemistry. The ecoregion approach is based on geographic characteristics, which may have a great influence on some lake characteristics such as lake formation, and therefore lake size, depth, and basin shape. This geographic approach also considers land use activities, which may have a large impact on lake quality.

Cluster analysis was performed using a nonhierarchical disjoint Euclidean distance cluster analysis (SAS 1990) on logarithmically transformed major ions (Ca, Mg, Na, K, SO_4^{2-}, and Cl-). Alkalinity was not included in the cluster analysis because of its high multi-colinearity with Ca and Mg, and some questions of data quality concerning the alkalinity measurements based on ion balance calculations. Clusters were determined by an iterative algorithm for minimizing the sum of the squared distances from the cluster means. The maximum number of iterations from competing cluster seeds was ten, and five clusters of lakes were identified. If a lake had a missing value for a variable, the missing value was estimated by the cluster seed value. This procedure allowed all lakes to be classified even if values for some of the variables were missing. Mean statistics for selected chemical and physical parameters were estimated for each cluster (Table 2).

The cluster analysis approach was optimized to identify spatial patterns; constraining the analysis to five clusters revealed the best grouping with respect to the ecoregions. These cluster groups were easily identified as groups of dilute, moderate, coastal, hardwater, and saline lakes, and were mapped in order to assess their geographic distribution (Figure 2). The mean (and standard deviation) chemistry of each cluster is shown in Table 2.

Most lakes in the dilute group are located at high elevations (ca. 2000 m) in the Cascades or Blue Mountains (Figure 2). The bedrock types in these areas are andesitic basalts, granites in the Blue Mountains, and other rocks resistant to weathering. These lakes tend to be small and have low ionic concentrations. The maximum conductivity in the dilute group is 18 µS/cm. By looking at the chemistry of these lakes, it is clear that not all lakes in the Cascade ecoregion are part of the dilute cluster. Some of these very dilute systems are located in the Blue Mountains although none are found in the East Cascades Ecoregion (Figure 2).

Lakes and reservoirs in the moderate group (Figure 2) have an average alkalinity of 384 µeq/L (Table 2). These lakes are geographically more dispersed than the dilute lakes (Figure 2) and are located in lower elevations in the Cascades, Eastern Cascades, the Willamette Valley and Eastern Oregon. The average lake size is larger than lakes in the dilute lake group. These lakes are also generally located over andesites and granites, but because of their elevation, they probably have larger watersheds with deeper soils.

The hard water group includes lakes and reservoirs with higher base cations. These lakes are moderate to large in size; most occur at lower elevations (~ 560 m). The hard water lakes are generally located over sedimentary bedrock and/or alluvial surficial deposits (Figure 2). Some of these lakes are located in areas of basalt overlain by loess, but occur across eastern Oregon, and are not associated with a particular ecoregion.

Coastal and Willamette Valley lakes were identified as a unique cluster (Figure 2). The chemistry of these systems is similar to those in the moderate cluster (Table 2); the feature distinguishing the two is the higher concentration of Na and Cl in the lakes of this cluster. The few lakes located in the Willamette Valley Ecoregion may be influenced by anthropogenic more than oceanic sources of Na and Cl. Only one of the moderate lakes was located in the Coastal Ecoregion.

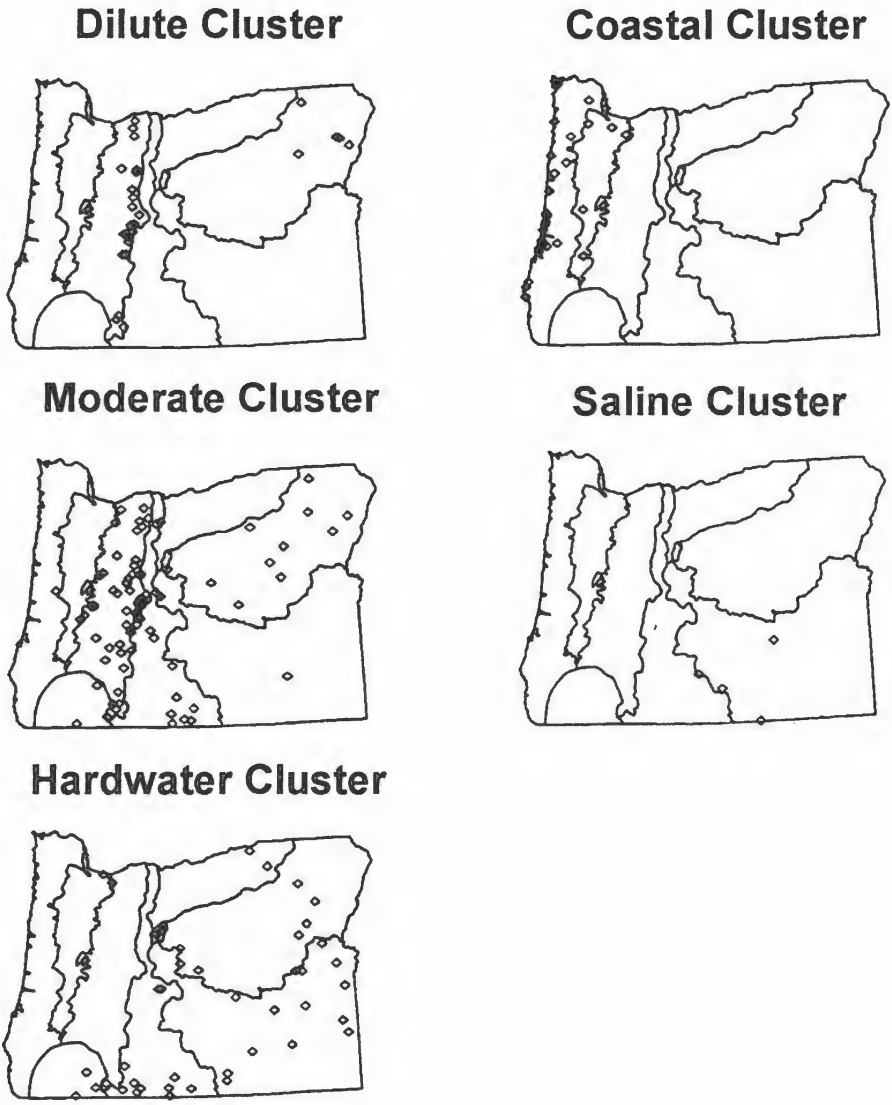

Figure 2. The geographic distribution of lakes in the five clusters, along with the ecoregion boundaries of the state.

The saline group consists of a few lakes with high conductivity and salinity (Figure 2). The range of Na concentration is 23,098 to 529,678 μeq/L, (mean conductivity of 13,837 μS/cm). The lakes are located in the south central Oregon desert (Figure 2); all are located in the High Desert Ecoregion. The bedrock composition in these areas is typically basalt with sodic soils.

These comparisons demonstrate that although some chemical characteristics may predominate in a given ecoregion, defining ecoregion boundaries is not synonymous with identifying lake water chemistry. Whereas dilute lakes are found at high altitude, they are accompanied by moderate and hardwater systems throughout the mountainous ecoregions of Oregon. While further delineation

of ecoregions into subregions may result in more specific delineation of lake chemical characteristics, the dilute and moderate cluster overlap suggests that this would be a difficult task.

Oregon lakes are impacted by non-point rather than point source pollution, as there are no longer any point source discharges to lakes. Thus management considerations for the problems evident in Oregon lakes relate to land and lake use practices, and require changes in these practices in order decrease pollution inputs to lakes. In large part these changes depend more on the land use activities than on lake chemistry itself. Almost all of Oregon's lakes face similar problems of eutrophication and sedimentation. However, the sources of these pollutants likely differ among ecoregions. For example, rangeland associated problems are more common in eastern Oregon, whereas problems related to increased development are more common in the western part of the state. Thus, while restoration of riparian areas and practices to decrease erosion should be adopted in both regions, the methods used to do so will likely differ. On the other hand, lakes with very sensitive chemistry may require more stringent management practices to achieve the same level of protection as less sensitive lakes. For example, Notasha and South Heavenly Twin Lakes may suffer more from trail and riparian zone erosion, than Lakes Elizabeth, Liza, Isherwood and North Heavenly Twin (Eilers et al. 1996b), simply due to differences in water quality. To be most effective, management plans should address local issues in terms of both land use activities, and lake and watershed sensitivity to perturbation.

Conclusions

Overall, lake water chemistry in Oregon is very diverse but spatial patterns are readily apparent. Some distinctions can be seen in average water chemistry among the eight ecoregions. The Cascade ecoregion contains the most dilute lakes, while the saline systems are found in the High Desert Region. Hardwater systems are more common in the ecoregions east of the Cascade range; the East Cascades, Columbia Plateau, and in the Klamath Region to the south. Coastal lakes have moderate chemistry, with somewhat higher salt concentrations. The results of a cluster analysis that grouped lakes based solely on chemistry also demonstrated a geographic distribution of lake chemistry, that was not dissimilar to the ecoregion boundaries, while concurrently demonstrating that lake location in a given ecoregion indicates little detail about its' chemistry. For instance, dilute lakes are located in alpine areas of the Cascade ecoregion, but selection of any single Cascade lake may not identify a dilute system. Lakes are impacted by pollution from non-point sources, so ecoregion descriptions provide important background information about land use, topography, and climate, that may provide a starting point for the development of detailed local management plans to protect Oregon's lakes and other surface waters.

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Recent Paleolimnology of Devils Lake, Oregon

Abstract

A study of the sediments in an eutrophic Oregon coastal lake, Devils Lake, was initiated to assist in management decisions regarding lake restoration. Recent limnologic changes in the lake were determined through examination of the sediments and measurement of lake bathymetry. A 1.5 m long core, collected near the lake center, was analyzed for percent water, loss-on-ignition, nitrogen, phosphorus, and diatoms. The age of the sediments was measured using ^{210}Pb for the upper sediments and ^{14}C for the lower sediments on a total of three cores. The upper 40 cm of sediment represented 140 years of accumulation. The age of sediments at the base of three cores ranged in age from 2030 (± 80) b.p. (core D 1.5 m) to 2870 (± 80) b.p. (core A 1.0 m) in the lake center. Marine sand was present at the base of core A, which was most likely derived from a tsunami. The analysis of diatoms in the sediments showed a very diverse flora with almost 250 taxa identified. The dominant diatom taxa changed relatively little throughout most of the last 140 yrs, suggesting that the lake was productive prior to recent development. Most of the changes in diatom taxa occurred in the last several decades and involved subtle changes in the less abundant taxa. A major erosional event occurred about 1912 (± 8 yr) causing a 5-fold increase in sedimentation rate based on ^{210}Pb dating. Sediment accumulation rates returned to pre-1900 rates in the 1920's and 1930's, but increased again in the last several decades. The major increase in sedimentation rate in the early part of the century corresponded to periods of intense storms which coincided with early development activities. The more recent increases in sedimentation rate which caused a loss in lake volume apparently resulted from a combination of urbanization and logging.

Introduction

Devils Lake is an eutrophic lake located in Lincoln County, on the central Oregon coast. Coastal lakes, such as Devils Lake, have been popular sites for residential and recreational development. The lake was formed by natural accumulation of beach sand impounding water at the outlet of the D River. Physical properties of the lake and watershed and water quality characteristics of the lake are summarized in Table 1. Surface water concentrations of total phosphorus and chlorophyll *a* averaged 60 and 41 µg/L, respectively in recent years (CH2M HILL 1992). Additional descriptions of the lake are available in Johnson et al. (1985). The lake exhibits abundant growths of macrophytes and occasional phytoplankton blooms. The lake has been the subject of several investigations over the previous 20 years (Kavanaugh 1973, Larson 1974, Shulters 1974, Meyerhoff 1977, Kramer, Chin, and Mayo 1983, Thomas et al. 1990, CH2M Hill 1992). Perceived water quality problems in Devils Lake, in addition to the visible growths of aquatic plants (especially *Myriophylum spicatum*), include occasional depletion of dissolved oxygen in the deeper waters, high nutrient concentrations, and an accelerated sedimentation rate. The primary action taken in response to these conditions has been to stock the lake with triploid (sterile) grass carp (*Ctenopharyngodon idella*) in 1986, 1987, and 1993 in an effort to control the excessive growth of macrophytes. Only modest reductions in the macrophytes occurred through 1992 (CH2M Hill 1992); however, major reductions in macrophyte biomass were observed in 1994 and 1995 (Dave Wagner, Devils Lake Water Improvement district, pers. comm.).

Although there was a strong perception by local residents that conditions in the lake had recently deteriorated, there were few historic data to support this view. The purpose of the study reported here was to satisfy the need for historical information on Devils Lake to aid in decisions regarding restoration efforts.

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TABLE 1. Devils Lake physical and water quality characteristics.

Physical Characteristics			
Lake Area (ha)	270.7	Lake elevation (m, msl)	3.05
Watershed area (km^2)	60	Lake volume (m^3 x 10^6)	6.14
Mean depth (m)	2.3	Annual Precipitation (m)	2.3-2.8
Maximum depth (m)	5.8		
Water Quality Characteristics (Units are in µM except as noted)			
pH (s.u.)[a]	8.09	Alkalinity[a]	448
Ca[b]	117	TP[a]	60
Mg[b]	128	SO_4 [b]	33
Na[b]	461	Cl[b]	440
K[b]	8	NO_3 [a]	1.3
Transparency (m)	2.1	SiO_2 [a]	95
Chlorophyll *a* (µg/L)[a]	41.4	Conductivity (µS)[a]	103

[a] CH2M Hill 1992
[b] Johnson et al. 1985

Methods

Sediment samples were collected from Devils Lake using a 5-cm diameter piston corer with a tube length of 2.5 m. The cores were collected from anchored rafts by placing the corer above the sediments and forcing the cylinder into the sediments using push rods until resistance prevented further penetration. This resulted in retrieval of sediment cores of about 1.5 m. Each core was inspected immediately for signs of disturbance caused by failure to capture the topmost sediment and for possible loss of sediment from the bottom of the core during core extraction. Four cores (A-D) were collected from several locations in the lake (Figure 1). Cores A, B, and C were collected on 14 February, 1993, and core D was collected on 30 May, 1993. Based on the quality of the initial analyses of the cores, core D was selected for more intensive analysis.

In addition to percent water and loss-on-ignition (LOI), subsamples of the sediment from core D were analyzed for lead-210 (^{210}Pb), total Kjeldahl nitrogen (TKN), total phosphorus (TP), and diatom species composition. Material from selected intervals was first analyzed for ^{210}Pb to ensure that the age of the sediments could be determined with confidence and to assess what portions of the core to analyze in greater detail. This procedure was necessary to ensure that the pre- and post-settlement periods were adequately represented in the core. Once the preliminary ^{210}Pb results were obtained, additional sediment intervals were analyzed to refine the sediment dating. ^{210}Pb activity was measured through its granddaughter product ^{210}Po, with ^{208}Po added as an internal yield tracer. The polonium isotopes were distilled from 0.2-1.3 g dry sediment at 550° C following pretreatment with concentrated HCl and plated directly (without HNO_3 oxidation) onto silver planchettes from a 0.5 N HCl solution (modified from Eakins and Morrison 1978). Activity was measured for 1-6 x 10^5 s with Si-depleted surface barrier detectors and an Ortec Adcam® alpha spectroscopy system. Unsupported ^{210}Pb, which is the ^{210}Pb derived from atmospheric sources, was calculated by subtracting supported activity, which is the ^{210}Pb produced from ^{226}Ra in the sediment, from the total activity measured at each level; supported ^{210}Pb was estimated from the asymptotic activity at depth (the mean of the lowermost samples in a core). Dates and sedimentation rates were determined according to the constant rate of supply model (Appleby and Oldfield 1978) with confidence intervals calculated by first-order error analysis of counting uncertainty (Binford 1990).

Sediment intervals from the base of cores A, C, and D were analyzed using ^{14}C techniques to estimate the overall sedimentation rate. Sample preparation and analyses were performed by Beta Analytic, Inc. using methodology described by Tamers (1975). Sediment from the following intervals was analyzed to achieve sufficient carbon for measurement: core A (92-100 cm); core C (146-154 cm); and core D (144-150 cm). The sediments were dispersed in deionized water, sieved to remove rootlets, and rinsed in hot acid. Neither rootlets nor carbonates were observed in any of the samples. After drying and final inspection, the portions of each were repeatedly combusted until adequate

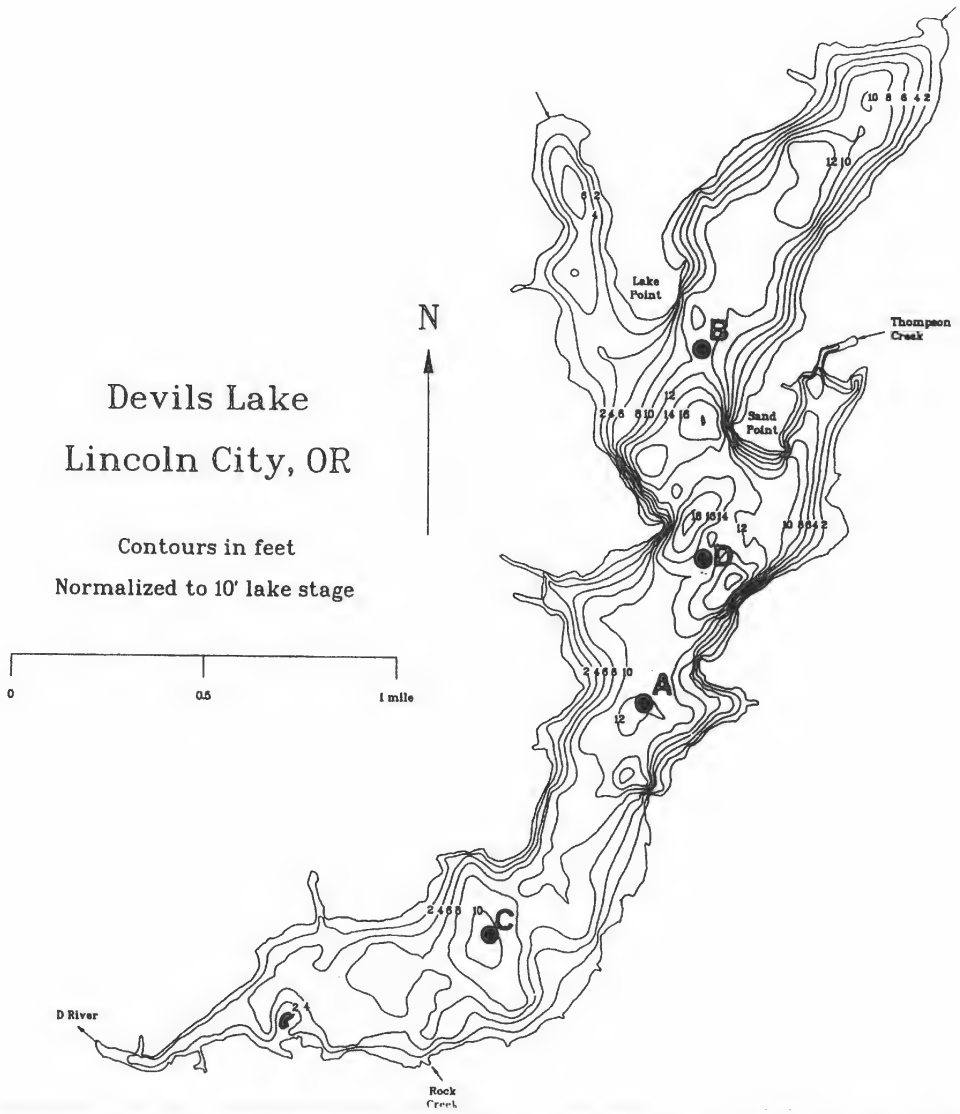

Figure 1. Bathymetric map of Devils Lake measured on 28 January 1994 using the methodology of Gubala et al. (1994). Coring sites (A-D) are located on the map. Lake area is 270.7 ha.

carbon dioxide was collected for analysis. All carbon in the sediment was assumed to be type C3 (terrestrial wood) for the purposes of dating.

Nitrogen in sediments was analyzed using a modified total Kjeldahl nitrogen (TKN) digestion (Method 351.1, EPA 1979) except that copper sulfate and sodium sulfate were substituted as catalysts in place of mercuric sulfate and potassium sulfate. Total phosphorus (TP) was measured using an ascorbic acid reaction spectrophotometrically in a 1 cm cell (Method 365.1, EPA 1979). Organic matter was estimated by LOI (Dean 1974).

The preparation of sediment samples for analysis of diatom fossils required special measures

because of the poor preservation of diatoms. Meyerhoff (1977) was unable to find a sufficient number of adequately preserved diatom frustules to complete his historical reconstruction of Devils Lake. Sediments from multiple cores and intervals were used to test for the presence of diatoms at various sediment intervals and to develop methods for slide preparation. One cubic centimeter of sediment was digested in a microwave oven with nitric acid. Diatom suspensions were settled onto cover slips in Battarbee trays and analyzed using a light microscope at 1000X magnification. A counting goal of 500 diatom valves per slide was established and achieved for most intervals. Counts of less than 500 valves were obtained for intervals 27, 30, 33, 39, and 42 cm. An insufficient number of diatoms in these intervals was attributed to an abundance of inorganic particles that "diluted" the diatom remains, although silica dissolution reactions involving aluminum and ferric oxyhydroxide reactions cannot be ruled out (cf, Nriagu 1978). Diatoms were identified to the lowest possible taxa using taxonomic protocols established in the PIRLA (Paleoecological Investigation of Recent Lake Acidification) project (cf, Charles et al. 1990).

A revised bathymetric map was prepared using a SONAR-GPS methodology developed by Gubala et al. (1994). Data for the creation of a bathymetric map for Devils Lake was collected on 28 January 1994; the staff gage height at the outlet was 3.018 m. A 200 kHz, 3.5° transducer was configured to acquire data at 3-second intervals. Average boat speed during data collections was about 5 to 6 m/s. All data were normalized by lake stage and expressed as depth relative to a lake stage of 3.048 m. Measurements of bottom reflectivity from the SONAR measurements also were recorded to provide an indication of changes in relative hardness of the sediment.

Results

Bathymetry and Reflectively

The bathymetric map of Devils Lake completed for this study shows a complex bottom profile with several depressions not previously identified (Figure 1). The maximum depth measured in Devils Lake was 5.8 m. The SONAR signal used to record lake depth also was evaluated with respect to signal strength, referred to as reflectively. Changes in lake bottom reflectivity can be used to evaluate spatial patterns in sediment composition such as differences between sand and organic sediments. The reflectivity values for Devils Lake ranged from 13 to 16 (relative intensity) throughout the lake. The values are indicative of relative signal strength and vary among lakes depending on the initial instrument settings used in optimizing the SONAR signal for a given application. The relatively small difference in reflectivity was considered insignificant. No spatial patterns were observed in these data, indicating that the physical properties of the surface sediments were relatively uniform.

Physical Characteristics of the Sediments

Cores B, C, and D were visually similar to one another and were about 1.5 m long. Core A, collected from the deepest location near the center of the lake, was only 1.0 m long but was noteworthy because of the distinct layer of sand present at the base of the core. The sand was relatively uniform and light tan, giving it the appearance and consistency of marine-derived sand. Although the sediments lacked varves, there were visible differences in sediment composition. All four cores had similar consistency at the top (~ 12 cm) with flocculent, brown organic-rich material, grading into sediment with greater plasticity and firmness. Sediment below 110 cm could usually be separated into non-cohesive portions. The sediment from 12 cm to 24 cm appeared brown (iron colored). The sediment had a distinct grey-green appearance from about 24 cm to the base of the cores, becoming darker green with increasing depth. Unidentified plant rhizomes were abundant in the cores below 100 cm. The water content in core D decreased down through the sediment from 93% at the surface to 79% at 150 cm; however, this trend was punctuated by portions of the core that showed minor reversals of 3 to 4% in the overall pattern.

Sediment Dating

The activity values of ^{210}Pb in core D were at supported (background) levels below 40 cm with an average supported activity of 0.60 pCi/g (Figure 2a). Although a core of 150 cm length was collected, the dating shows that the upper 39 cm of sediment represents the last 140 years of lake history (Figure 2b). The sediment interval from 33 to 39 cm represents the pre-settlement period from about 1850 to 1880. Sediment accumulation in

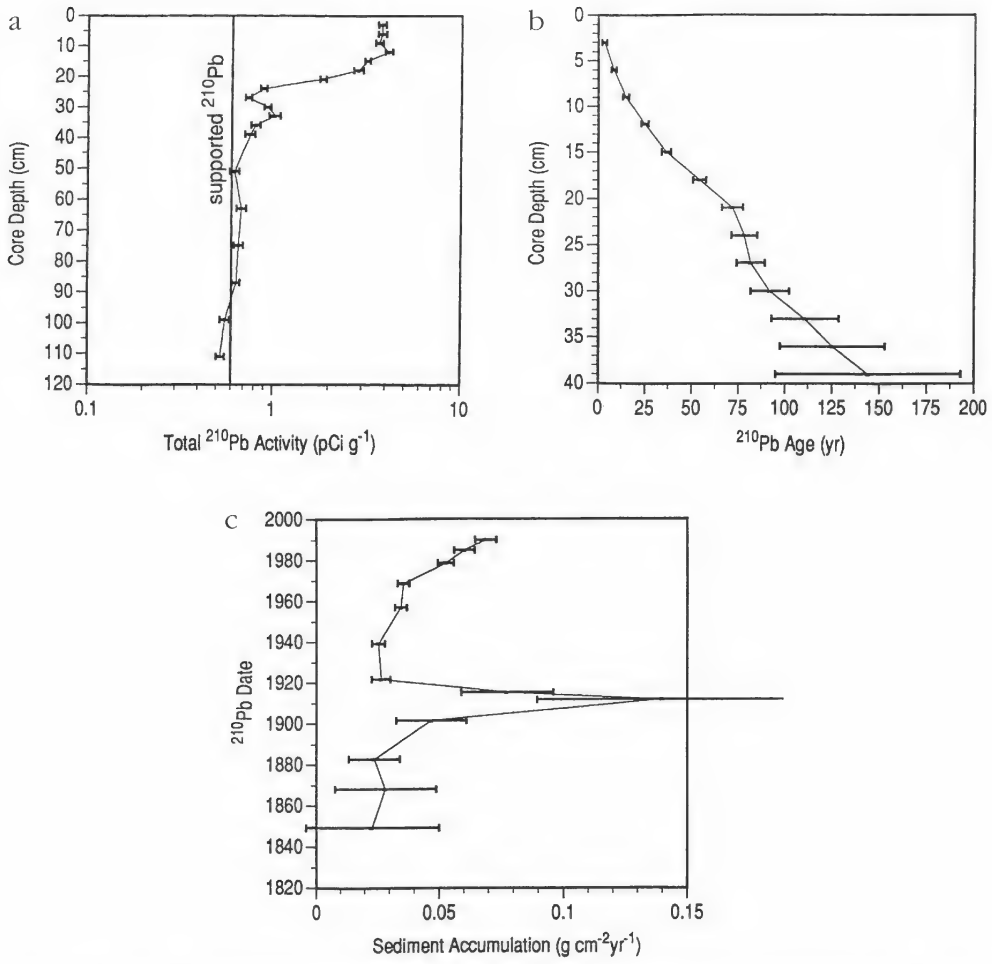

Figure 2. (a) Total ^{210}Pb activity (pCi/g) for Devils Lake core D; (b) Age of sediments estimated from ^{210}Pb activity versus sediment depth in Devils Lake, core D. The horizontal lines associated with each observation represent the uncertainty (1 sd) in the age of the sediments; c) Sediment accumulation rate (g/cm^2/yr) in Devils Lake, core D, versus sediment date. The horizontal lines associated with each observation represent the uncertainty (1 sd) in the sediment accumulation rate.

this period was about 0.025 g/cm^2/yr, increasing to a maximum of 0.14 g/cm^2/yr around 1912 (±7.6 yrs), which was over five times the pre-settlement rate (Figure 2c). Sediment accumulation rates decreased to near pre-development sediment accumulation rates of 0.026 g/cm^2/yr during the 1920's to 1940's. In the 1950's, the sediment accumulation rate began increasing again to values which are currently about 2 1/2 times the pre-settlement rate.

The long-term age at the base of the cores was determined by ^{14}C measurements on three of the four cores. The bottom of the cores ranged from about 2000 to 3000 years of age (Table 2). If we examine the sediment accumulation rate below 33 cm in core D, the average rate of sedimentation would be 0.0113 g/cm^2/yr, or about one-half of the minimum sedimentation rate measured in the upper portion of the core. Sedimentation rates below 33 cm in Devils Lake of 56 cm/per thousand

TABLE 2. Radiocarbon dating of sediments in Devils Lake, Oregon.

Core	Sediment Depth (cm)	Radiocarbon Date (Years BP)	Analytical Precision[a] (Yr)	Calendar Equivalent Ages[b]	Average Accumulation Rate (cm/kyr)
A	92-100	2870	± 80	1270 BC to 830 BC	33.4
C	146-154	2600	± 70	850 BC to 530 BC	57.7
D	144-150	2030	± 80	200 BC to 140 AD	72.4

[a] 1 standard deviation

[b] assuming type C3 carbon (terrestrial wood)

years (cm/kyr) are comparable to two cores collected from Lake Washington which showed linear accumulation rates of 51 cm/kyr and 55 cm/kyr (Karlin and Abella 1992). The ^{14}C results provide additional confirmation that current sedimentation rates are considerably greater than natural rates and could range from 2 to 5 times pre-development rates depending on whether the ^{210}Pb or ^{14}C dates are used.

Sediment Chemistry

Loss-on-ignition (LOI) provides a gross measure of sediment composition, particularly organic matter. Sediments high in inorganic materials such as clay will exhibit low LOI values, whereas sediments with a high proportion of decomposing organic matter will exhibit high LOI values. A comparison of four cores (A-D) collected in Devils Lake shows that cores A, B, and D are quite similar for the past 150 years, but deviate from one another below 50 cm (Figure 3). Core C collected closest to the boat launch on the south end of the lake, has a much higher organic content than the other three cores. Whereas cores A, B, and D reach local minima in LOI near 27 cm, sediment from core C tends to increase in LOI below 27 cm. These results indicate that core D is reasonably representative of the general stratigraphy (as represented by LOI) in the northern two-thirds of the lake, but core D may not be indicative of changes occurring in the southern portion of the lake.

Major trends in the nutrient status of Devils Lake were investigated by measuring the nitrogen and phosphorus content of the sediment. Both total Kjeldahl nitrogen (TKN) and total phosphorus (TP) concentrations reached a maximum at 24 cm and exhibited fairly stable values down to 39 cm (Table 3). Two deep sediment samples showed much greater concentration of TKN, possibly because of the rhizomes present. TP concentrations in the pre-settlement era were only about 20% of the maximum values observed at 24 cm. Thus, both TKN and TP concentrations in the sediments have decreased from the peak at 24 cm which corresponds to a date of 1915 ($\pm$ 6.9 yrs). The ratio of TKN/TP shows three distinct periods whereby the ratios from 0 to 15 cm (from present to 1957 $\pm$ 2.4 yrs) are between 3-4, the ratios from 18 to 30 cm (1939 $\pm$ 3.5 yrs to 1882 $\pm$ 17.9 yrs) are between 1-2, and the values to 42 cm are between 4-9. Most of the changes in the TKN/TP ratio can be attributed to changes in TP which showed a major increase in phosphorus that corresponds with the first records of modern settlement in the county (Steere 1951).

Diatoms

The sediment diatom assemblages are remarkably diverse. Up to 86 taxa were present in specific sediment intervals, with a total of 243 taxa recorded in the fourteen intervals analyzed from core D. The number of taxa decreased from 85 taxa in the surface sediments to 51 taxa at 42 cm, although this was largely an artifact of the total diatoms counted per interval. When the prescribed number of diatoms ($\geq$ 500) were counted, the number of taxa recorded was significantly ($p \leq 0.05$) greater than those intervals with counts less than 500. Several sections had an insufficient number of diatoms available for counting because of either dilution from sediment particles or possible dissolution reactions occurring in the sediments. When the observed number of diatom taxa are normalized to a standard number of valves counted, the expected number of taxa differs relatively little from the number of observed taxa for sections with $\geq$ 500 diatoms counted.

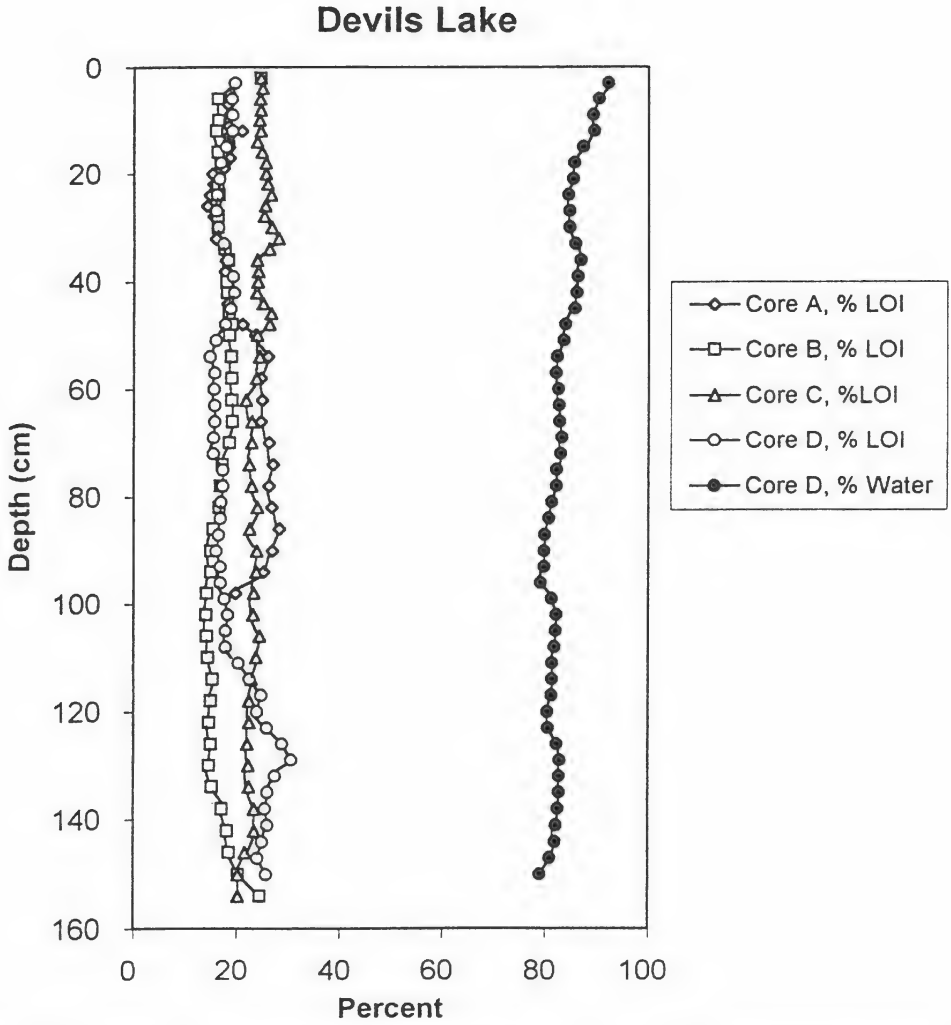

Figure 3. Percent water and loss-on-ignition (LOI) versus sediment depth (cm) in core D. LOI values are also shown for cores A, B, and C.

The most abundant seven taxa present in the sediments show only modest changes in relative abundance through the core (Figure 4). The most abundant taxon, *Cocconeis placentula* var. *lineata* shows a slight decline from 18-33 cm, but two intervals at 24 and 30 cm have relative abundances near 20%, which casts doubt on the significance of the apparent decline. *Fragilaria construens* var. *venter* is most abundant at intervals 18 and 21 (1939 and 1922, respectively), at a period when the sedimentation rate had decreased to near pre-industrial levels. *Fragilaria crotonensis* exhibited a trimodal distribution with peaks at 3, 12, and 39 cm. The major decline of *F. crotonensis* beginning at 33 cm precedes the accelerated sedimentation which begins at 30 cm.

Asterionella formosa is a species commonly found in highly productive lakes. With the exception of the observations from 39 cm, the species appears to display a gradual increase in abundance from historical times to present. *A. formosa* was the principal species associated with increasing

TABLE 3. Total Kjeldahl nitrogen (TKN), total phosphorus (TP), and the ratio of TKN/TP in Devils Lake, core D.

Sediment Depth (bottom of interval, cm)	Total Kjeldahl Nitrogen (TKN) (mg/g, dry wt)	Total Phosphorus (TP) (mg/g, dry wt)	TKN/TP
3	2.7	0.7	3.8
6	9.1	2.5	3.6
9	11.9	3.2	3.7
12	8.2	2.2	3.8
15	8.5	2.7	3.2
18	7.0	1.9	3.6
21	7.3	3.6	2.0
24	7.4	4.8	1.5
27	5.6	4.5	1.2
30	5.9	3.8	1.6
33	6.1	1.0	5.8
36	8.8	1.0	8.5
39	7.1	1.4	5.1
42	7.3	1.6	4.6
72	6.3	1.1	5.7
102	5.4	0.6	8.4
123	8.8	0.5	17.4
150	7.8	0.3	22.4

watershed disturbance for lakes in western Washington (Brugam and Vallarino 1989). In some of their study lakes, relative abundance of *A. formosa* increased from 0 to over 60%. The relatively small changes in abundance for *A. formosa* observed in Devils Lake suggest only slight changes in productivity during the last century.

Navicula radiosa shows a general decrease through the period of record. As observed with *A. formosa*, the interval that is a major exception to the overall trend occurs at 39 cm. *Fragilaria construens* var. *pumila* also exhibits a slight decrease, most of it occurring in the most recent sediments. In contrast, *Fragilaria pinnata* exhibits a slight increase in relative abundance. Whatever changes may have occurred in water quality in Devils Lake in the last century have not been great enough to cause pronounced changes in the dominant diatom species.

The information regarding the less abundant diatom species was assessed through multivariate statistical techniques. A principal component analysis (PCA) using all taxa present showed that the recent sediment samples (0-12 cm) were distinct from the diatom community in the deeper sediment samples (Figure 5). When cluster analyses (FASTCLUS, SAS 1988) is used to group the sediment intervals according to statistical similarity, we observe that the top interval (3) forms its own cluster (I) as do intervals 6, 9, and 12 (Cluster III). The remaining intervals form clusters that show little relationship to other sediment characteristics such as sedimentation rate or sediment nutrient concentrations. These data for the dominant diatom taxa suggest that the water quality in the lake, at least in the northern half of the lake, has not changed radically in the last century. However, the community composition shows more subtle changes among the less common species that may reflect some water quality change in the last three to four decades.

Discussion

There is local concern regarding accelerated watershed erosion and sedimentation in Devils Lake (Kramer, Chin, and Mayo 1983). The sediment accumulation since creation of the 1953 bathymetric map (Oregon State Game Commission

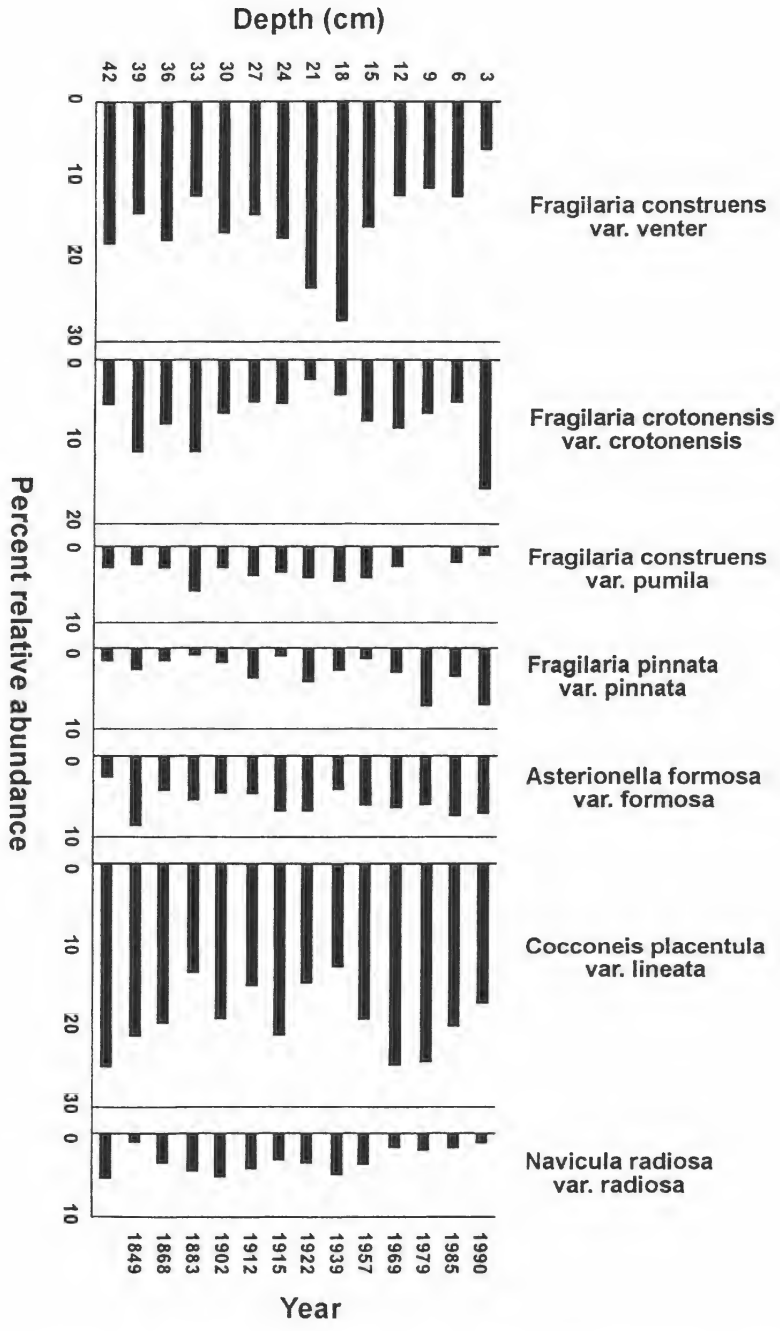
Depth (cm)
42 39 36 33 30 27 24 21 18 15 12 9 6 3
Fragilaria construens var. venter
Fragilaria crotonensis var. crotonensis
Fragilaria construens var. pumila
Fragilaria pinnata var. pinnata
Asterionella formosa var. formosa
Cocconeis placentula var. lineata
Navicula radiosa var. radiosa
Percent relative abundance
0 10 20 30
1849 1868 1883 1902 1912 1915 1922 1939 1957 1969 1979 1985 1990
Year

Figure 4. Relative abundance (% of total counts) of dominant taxa in Devils Lake, core D in the upper sediments (cm).

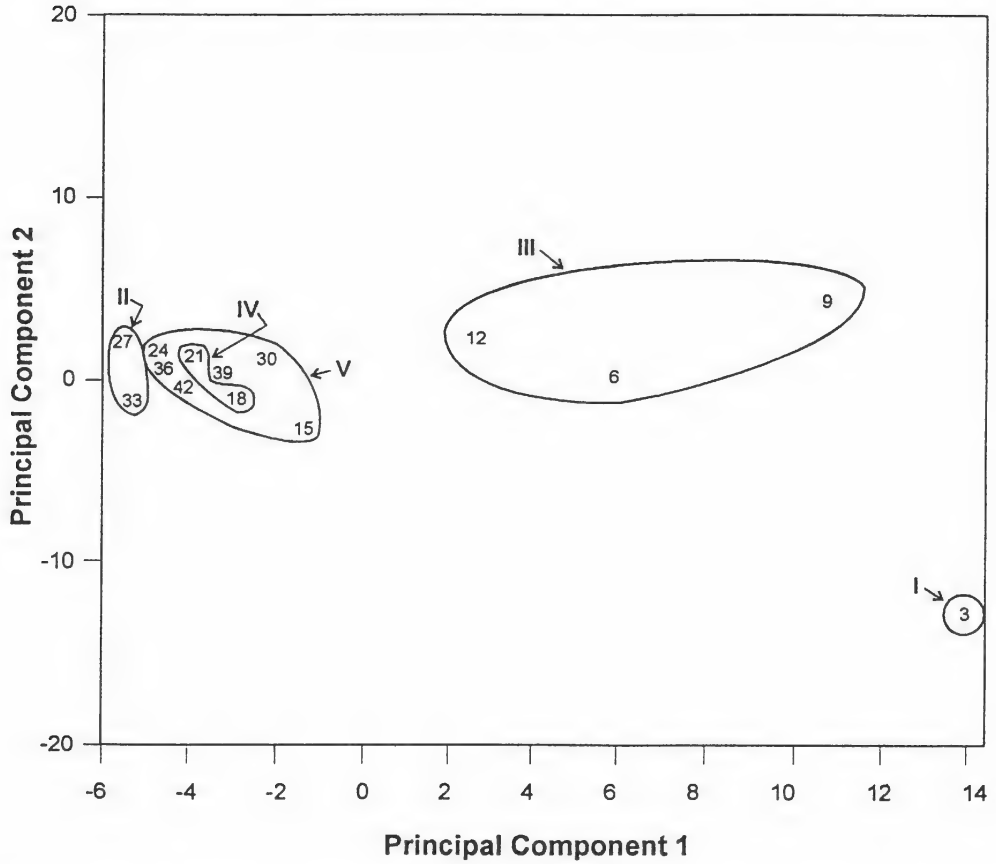

Figure 5. Principal component classification of diatom species composition in Devils Lake, core D for the first two principal components. The numbers refer to the sediment interval. Related diatom communities are indicated by the five clusters (I-V) encompassing the numbered individual sediment intervals. All 243 diatom taxa were included in the classification.

1953), computed on the basis of ^{210}Pb dating for core D, is only about 15 cm. If this estimate represents a reasonable lake-wide accumulation rate, the lake has lost about 4 x 10^5 m^3 or 6% of the previous lake volume over the last 40 years. However, the actual reduction in lake volume could be considerably different than that estimated on the basis of sediment accumulation at one site. Reports of shoaling in embayments following major storm events (see Johnson et al. 1985) suggest that deposition rates adjacent to inlets are greater than in the lake center. Thus, a 6% reduction in lake volume over the last 40 yrs may be an underestimate. Alternatively, if sediment focusing is occurring at this site, then the actual lake-wide sediment accumulation could be less than this estimate. An upper-bound estimate for loss of lake volume based on comparison of the current bathymetry with 1953 bathymetry is 26%.

The sediment reconstruction for Devils Lake is based largely on the results of one core, raising some concerns about the homogeneity of the sediments and the representativeness of core D. Both the SONAR reflectivity results and the LOI results from three other cores indicate relatively little variation in the physical composition of the sediments. However, some difference was noted in the LOI values between core C from the southern

portion of the lake and the remaining cores. The apparent lack of synchronism between core C and the remaining cores could be due, in part, to different influences in the southern portion of the lake. The decreases of LOI in core C near 40 and 60 cm may correspond with the decreases observed at 24 cm in cores A, B, and D. Site C favors a high sedimentation rate because of its proximity to Rock Creek which drains most of Devils Lake watershed. The southern end of the lake also was the discharge site for the Oceanlake sewage treatment plant from 1951-1970. Meyerhoff (1977) analyzed four 50-cm long sediment cores collected from 3 m to 6 m depths in Devils Lake. Sediments from the 6 m site (located near site D in this study) were analyzed in the greatest detail. There were only small variations in percent organic matter (LOI) and profiles were uniform ranging from 22 to 25% LOI in three of the four cores. This compares reasonably well with the values measured in this study which ranged from 15 to 25% in the upper 50 cm. Meyerhoff (1977) measured LOI values of 10% in one core collected from a lake depth of 3.5 m. This site appeared to be close to shore and may have received greater erosional inputs than the deeper sites.

Whether the differences in TKN/TP ratios among the intervals correspond to differences in *inputs* of nutrients or differences in *retention* of the nutrients cannot be determined with these data. It is possible that the apparent changes in the TKN/TP ratio are an artifact caused by differences in nutrient mobility in the sediments, rather than serving as an unaltered record of nutrient deposition (cf, Carignan and Flett 1981). Both N and P are mobile to some degree in sediment and their peak concentrations at 24 cm may reflect redox gradients rather than depositional history. The accumulation rates of TKN and TP peak in the early portion of the century, corresponding to the major depositional event. These data suggest that TKN and TP accumulation rates are associated with erosional inputs. Assuming that this is the cause, it is likely that most of these nutrients entered the lake in particulate form and were generally unavailable for uptake by aquatic macrophytes or phytoplankton. Regardless, the sediment profile provides dramatic evidence of the potential importance of major hydrologic events, not only on sedimentation, but on nutrient accumulation as well.

Meyerhoff (1977) also measured increased TP and TKN above 30 cm in the sediments. The increase in sediment TP concentrations peaked at 22 cm with values about three-fold greater than values measured near the base of the core. The increase in TKN was more gradual up to 6 cm, where a five-fold increase over base values was observed. Meyerhoff (1977) attributed the higher nutrient concentrations in the surface sediments to watershed activities which increased nutrient loads.

The ^{14}C dates for the three sediment cores show that long-term average sediment accumulation rates in Devils Lake are low, and appear to be greatest in the northern part of the lake. This is unexpected considering that the primary tributary discharges into the southern portion of the lake. However, the proximity of Rock Creek to the outlet may result in much of the sediment load depositing closer to the outlet or being transported to the ocean. Core C, collected near the southern end of the lake, exhibits a long-term average sedimentation rate about 25% less than core D. The core collected from the lake center, core A, is the shortest core, and exhibits the lowest sedimentation rate. The sand layer at the bottom of core A (and observed at the base of several other incomplete cores that were discarded) was noteworthy because of its distinctly marine appearance. Heusser (1960) collected a 7 m-long core through peat adjacent to the west shore of Devils Lake and estimated the age of the lake at 6,300 (± 275) BP using ^{14}C dating. Heusser (1985) also noticed that sand was interbedded in the lake sediments, which he viewed as an indication the lake became estuarine at times. More recent studies of lake and estuaries along coastal Washington (Atwater 1987, 1992; Jacoby et al. 1992; Karlin and Abella 1992; Schuster et al. 1992) and Oregon (Darienzo and Peterson 1990, Nelson 1992, Nelson et al. 1994, Darienzo et al. 1994) indicate that at least some of these lake sediment sand layers were derived from tsunamis generated by earthquakes.

Devils Lake has received numerous inputs from anthropogenic activities in the last 100 years including erosion from logging and development, poorly treated effluent from a sewage treatment plant, and runoff from livestock and urban areas. In addition, the lake was treated with rotenone and stocked with warm-water fish species, trout,

and herbivorous carp (Dave Wagner, Devils Lake Water Improvement District, pers. comm.). The population of the area has grown from a small group of native tribes in the 1800's to the current community of Lincoln City with a population over 5000.

We were unable to identify conclusive evidence of anthropogenic disturbance in the early part of the century that might explain the dramatic increase in sedimentation observed between 1900 and 1920. There is evidence that the settlement of the Devils Lake area began in the 1890's, but it is unclear what the major activity associated with the early settlements was in this watershed. There are accounts of homesteaders with livestock present in the area as early as 1909. Logging was beginning along the Oregon Coast during this period and the timber industry was greatly stimulated by demand for lumber products following the 1906 earthquake in San Francisco. However, specific evidence for intensive logging in the Devils Lake watershed is somewhat conflicting. Examination of the nearshore area shows only a small number of extremely large stumps, suggesting that little old growth forest was present in the watershed in the late 1800's. A review of the 1900 forest cover maps (scale 1" = 2 mi.) for the area shows the Devils Lake watershed classified primarily as recently burned. The 1914 forest classification map (scale 1" = 6 mi) also shows most of the watershed as "burnt with restocking." However, a more detailed 1936 (scale 1" = 0.66 mi.) classification represents the shoreline and lowland area of the watershed as large spruce hemlock (forests containing >50% by volume either western hemlock or Sitka spruce, trees from 20 to 24 in diameter). Much of the upland portion of the watershed is classified on this map as large second growth Douglas fir (forests, not yet mature, containing >60% Douglas fir where the majority of volume in trees 20-40 in. diameter). The immature Douglas fir stands are consistent with the earlier forest fire history, but the lowland spruce/hemlock forest suggests a different situation than that represented on the 1900 and 1914 small-scale maps.

Historical precipitation records earlier than 1928 are unavailable for this area. Precipitation records for Corvallis, located about 70 km southeast from Devils Lake, indicate that the largest three-day precipitation event recorded for the region occurred 17-19 January 1911 when 16.5 cm was recorded (Office of State Climatologist, Corvallis). Precipitation at the coast averages about 40-60% greater than in Corvallis, suggesting that this event could have been in excess of 25 cm at Devils Lake. Precipitation in 1909 also appears to have been well above normal, at least for October and November (Steere 1951).

The high precipitation events in 1909 and 1911 provided opportunities for accelerated erosional inputs into Devils Lake. The possibility that the erosion which occurred circa 1910 was entirely natural is low in view of the low long-term sediment accumulation rate based on the ^{14}C measurement and the absence of periodic erosional events that might have been associated with high precipitation events. Furthermore, the greatest floods in western Oregon in modern history (1861, 1890, 1943, 1945, and 1964) do not correspond with the high sedimentation periods observed in the Devils Lake sediment. We conclude that the high sedimentation rate in the early 20th century was caused, in large part, by watershed activities.

Although the historical peak in sediment accumulation is dramatic, the sediment accumulation rate quickly returned to pre-settlement rates. Of greatest interest with respect to current management of Devils Lake is the trend in the last three to four decades which shows a steady increase in the rate of sediment accumulation (Figure 6). The cumulative sediment accumulation in the last three decades exceeds the total sediment accumulation from 1900-1920. The results of this paleolimnological reconstruction suggest that lake management efforts should focus on identifying important land use contributions to watershed erosion and controlling these erosional inputs. This appears to be consistent with plans being implemented by the Devils Lake Watershed Improvement District (Wagner 1994).

The biological history of the lake, as reflected in the sediment diatoms, shows a more subtle pattern. The major diatom species have shown only minor changes in relative abundance, although several species display apparent trends. Judging from the diatom species composition, it appears that the lake has been productive for at least the last 150 years and probably much longer. A statistical analysis of the diatom community shows that the species composition in the most recent sediments (i.e. last 25 years) differs, particularly among the less common species, from diatoms in the deeper sediments.

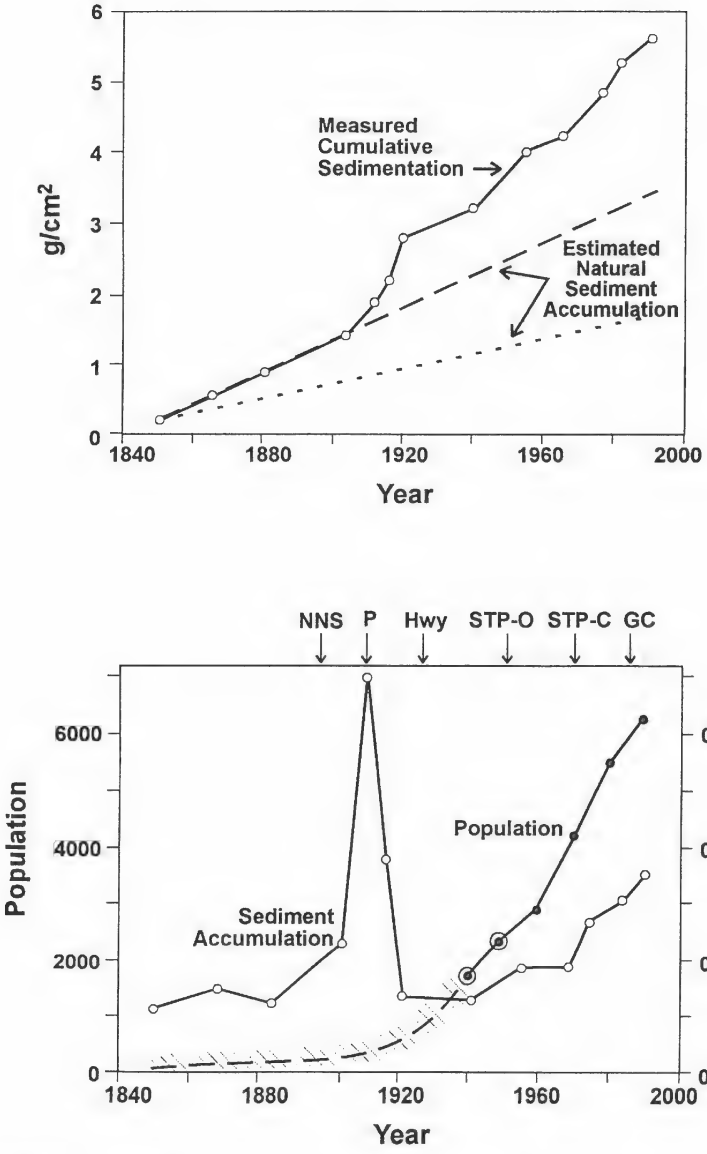

Figure 6. Major changes in the sediment history of Devils Lake as indicated by the sedimentation rate (—o—) compared to population ---•--- for the Lincoln City area. (a) The top panel shows the measured cumulative sedimentation for Devils Lake (solid line) compared to cumulative sedimentation under natural conditions assuming rates calculated from 1850 to 1900 using ^{210}Pb (middle line) and sediment accumulation calculated from ^{14}C dating techniques (bottom line). (b) Population for 1960 and later is based on census data for the city. Population for 1940 and 1950 was estimated as a percentage of Lincoln County census data. Population ranges prior to 1940 are estimates. The letters at the top refer to the following: [NNS] non-native settlement begins; [P] largest 3-day precipitation event recorded; [Hwy] highway to Devils Lake completed; [STP-O] sewage treatment plant begins discharging to lake; [STP-C] sewage treatment plant closed; [GC] first stocking of grass carp.

The sediment data suggest that the greatest changes in the biological characteristics of Devils Lake occurred in the last three decades, although the major physical changes occurred earlier in the century. However, the current trend in sedimentation rate indicates an accelerated rate of watershed erosion. If the rate of erosion continues to increase, it will cause a serious loss in lake volume over the next several decades. Unchecked sedimentation will continue to provide additional habitat for macrophytes by increasing the littoral area in the lake and resupplying macrophytes and phytoplankton with nutrients.

The increased sedimentation in Devils Lake may be typical of problems occurring in other Oregon coastal lakes. A number of these lakes have experienced changes in watershed activities similar to those reported here for Devils Lake leading to reported problems associated with eutrophication (Daggett et al. 1996). For other lakes, the pressure to log and develop the forested watersheds is more recent. The results from Devils Lake indicate that future problems in these coastal lakes could be minimized by initiating more aggressive programs to control accelerated erosion and nutrient export from the watersheds. Failure to control these activities will result in further loss of lake volume and increased likelihood of problems associated with eutrophication.

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Eutrophication of Mercer, Munsel, and Woahink Lakes, Oregon

Abstract

Mercer, Munsel, and Woahink Lakes are part of a unique assemblage of dune lakes situated near the city of Florence on the central Oregon coast. Combining results from two independent studies, this paper presents evidence suggesting that these lakes have become more biologically productive since European-American settlement, apparently as the result of human activities. These lakes are representative of lakes in the area and changes occurring here may be indicative of more geographically widespread changes in lake conditions. Currently, Mercer Lake is very productive (mesotrophic to eutrophic), Munsel Lake is moderately productive (mesotrophic), and Woahink Lake is slightly productive (oligotrophic).

Studies, conducted at each lake since 1938, have become more frequent and comprehensive since 1970. Data collected between 1938 and 1970 were limited in scope and focused on fishery production. Since 1970, research has focused on limnological and water quality studies and water quality parameters have included primary productivity, chlorophyll *a*, phytoplankton, zooplankton, nutrients, and sediment chemistry.

Examination of data for those parameters measured consistently between 1938 and 1992 (temperature, dissolved oxygen, and Secchi Disk transparency) shows no evidence of eutrophication, or suggests an improvement in water quality (increases in Secchi Disk transparency at Woahink Lake), while more sensitive water quality parameters (primary productivity, chlorophyll *a,* and sediment chemistry) suggest that eutrophication has occurred.

A number of factors point to eutrophication. Between 1970 and 1991, phytoplankton primary productivity rates have increased substantially in all three lakes. In addition, at Mercer Lake, chlorophyll *a* concentrations have increased, as have concentrations of organically-associated Fe and the relative numbers of *Fragilaria construens* in sediment cores. In Woahink Lake, increases in sedimentation rates and densities of selected zooplankton species indicate increased biological productivity.

Introduction

Limnologists and area residents are concerned that human activities are negatively impacting the water quality of Mercer, Munsel, and Woahink Lakes. This concern is based on the knowledge that a lake is the ultimate sink for nutrients, sediment, and pollutants generated by human activity in the watershed (Likens 1985). The study lakes are situated in an area of soils that are very susceptible to human impacts (Christensen and Rosenthal 1982). In each watershed, activities that remove vegetation and disturb soil, such as clear-cut logging and development, have occurred. Compounding these stresses is the increasing development of prime lakefront and watershed properties resulting from the rapidly expanding population in the Florence area. The ecology of these three lakes is representative of many lakes in this area and changes occurring here may be characteristic of more widespread changes occurring in lake water quality on the central Oregon coast.

While human activities have clearly altered the watersheds of the lakes, the impact of the activities on the lakes' water quality is less well known. This paper discusses evidence suggesting that the study lakes have become more biologically productive (eutrophic), apparently as a result of human activities, and provides additional, limnological information about each lake. These lakes were chosen by Daggett (1994) primarily because of the availability of data from 1938 through 1992, while Vogel (1994) selected the lakes as part of a statewide study. The lakes' historical data sets (1938-1993) were evaluated in an attempt to detect water quality changes over time and findings from the two most recent studies (Daggett 1994, Vogel 1994) independently corroborate the conclusions reached in this paper. Data collected in 1985 by Vogel (1994), in 1991 by Larson and Salinas (Daggett 1994), and in 1992 by Daggett (1994) were used to estimate each lake's current trophic state.

Study Area and Background

The study lakes, located on the central Oregon coast, are clustered around the city of Florence on the northern edge of the Coos Bay dunal sheet. The dunal sheet extends approximately 100 km between Heceta Head to the north and Coos Bay

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to the south and ranges in width up to 5 km, being bordered to the east by the foothills of the Coast Mountain Range and to the west by the Pacific Ocean. The sheet represents accumulated wind-blown sand that was deposited within the last 27,000 years on a section of ancient wave-cut terrace that was warped downward below sea level (Schlicker and Newcomb 1974). The study lakes, and many others in the area, originated as the combined result of a post-glacial rise in sea level and the subsequent impoundment of coastal river valleys by migrating sand dunes. These dune lakes are thought to be unique in the northern hemisphere because of their size range, large number, great variety, and close physical proximity (Larson 1991).

Each of the lakes has received periodic research attention since the first description of Woahink Lake by Evermann and Meek (1897). Studies conducted between 1938 and 1970 were primarily concerned with fisheries management (Griffiths and Yeoman 1938; Oakley 1962a,b; McGie and Breuser 1962). In contrast to current nationwide efforts to limit nutrient inputs and reverse eutrophication, Griffiths and Yeoman (1938) suggested that some of the less productive coastal lakes, such as Woahink, should be considered as candidates for nutrient enrichment to increase fish production. Since 1970 studies of the lakes have been primarily concerned with water quality or general limnological investigations (Larson 1970a,b, 1974; Malick 1971; Kavanagh 1973; Bryant 1979; Johnson et al. 1985; Sweet 1990a,b; Daggett and Petersen 1993,1994; Daggett 1994, and Vogel 1994). Researchers have consistently ranked Mercer the most productive and Woahink the least productive. The physical and conservative characteristics of these lakes are presented in Table 1 (from Johnson et al. 1985 except as noted).

TABLE 1. Selected physical, chemical, and biological parameters. (Physical parameters from Johnson et al. 1985 except as noted. Chemical and biological data from Daggett 1994. Limnological data collected at site of maximum depth).

	Mercer L.	Munsel L.	Woahink L.
Elevation (m)	9.8	27.4	11.6
Area (hectares)	145.3	44.5	331.9
Maximum Depth (m)	11.6	24.0(1)	20.7
Mean Depth (m)	7.1	9.3	9.9
Volume (m^3)	1.0×10^7	4.2×10^6	3.3×10^7
Area (<3.3 m)	13%	24%	17%
Watershed Area (km^2)	22.0	4.4	4.4
Retention Time (years)	0.33	1.0	1.2
pH (su) at 0.0 m (1)	7.9	6.5	6.8
pH (su) at 1.0 m above sediment (1)	6.2	5.3	5.8
Conductivity ($\mu S\ cm^{-1}$) at 0.0 m (1)	73	67	68
Conductivity ($\mu S\ cm^{-1}$) at 0.5 m above sediment (1)	142	140	74
Redox potential (mv) at 0.0 m (1)	82	96	77
Redox potential (mv) at 0.5 m above sediment (1)	-171	-130	121
Mean Chlorophyll *a* ($\mu g\ L^{-1}$)	17.4 ± 6.5 (1,3)	3.0 ± 2.5 (1,4)	1.9 ± 0.8 (2,5)
Mean 1993 Secchi Disk depth (m)	4.1 (n=11)	5.4 (n=13)	7.8 (n=21)
Total phosphorus ($mg\ L^{-1}$) at 0.0 m (2)	.02	.01	<.01

(1) Larson and Salinas 13 September 1991, published in Daggett 1994
(2) 23-24 June 1992
(3) 0, 5, 10 m
(4) 0, 5, 10, 15 m
(5) 0, 14, 16 m

Methods

Sample sites for Daggett (1994), Vogel (1994), and Larson and Salinas (Daggett 1994) were located at the deepest point of each lake. Vogel (1994) collected an additional sediment core in the northeast arm of Woahink Lake. Daggett (1994) sampled each lake twice during June and July 1992 and collected data and samples for temperature, dissolved oxygen, conductivity, chlorophyll *a*, total phosphorus, optical characteristics, and phytoplankton. Larson and Salinas (Daggett 1994) sampled Mercer Lake and Woahink Lake each twice during August and September 1991 and sampled Munsel Lake three times during August and September 1991, collecting data and samples for primary productivity, temperature, dissolved oxygen, pH, conductivity, redox potential, alkalinity, chlorophyll *a*, phytoplankton, and zooplankton. Vogel (1994) collected sediment cores at each lake between March and August 1985. Table 2 summarizes the types of data collected for the studies discussed in this article.

TABLE 2. Selected water quality variables investigated at Mercer, Munsel, and Woahink Lakes.

	Productivity	Phyto-plankton	Chlorophyll *a*	Zooplankton	Trace Metals	Temperature & Dissolved O	Nutrients	Secchi	Conduc-tivity	Redox Potential
Mercer and Munsel Lakes										
Griffith and Yeoman (1938)						X				
Kavanagh (1973)	X		X	X		X	X	X		
Larson and Salinas (1991)[1]	X	X	X	X		X		X	X	X
Daggett (1994)		X	X			X	X	X	X	
Vogel (1994)		X			X					
Woahink Lake										
Griffith and Yeoman (1938)						X				
Larson (1970)	X	X	X			X		X	X	
Malick (1971)				X		X				
Larson and Salinas (1991)[1]	X	X		X		X		X	X	X
Daggett (1994)		X	X			X	X	X	X	
Vogel (1994)		X			X					

(1) Reported in Daggett (1994)

Temperature, dissolved oxygen, pH, conductivity, and oxidation-reduction potential were measured *in situ* from lake surface to bottom using a Hydrolab model 8000. Additional temperature and dissolved oxygen, and conductivity profiles were measured *in situ* with YSI meters (model 158 and 33 SCT, respectively).

Water samples were collected at various depths with Van Dorn-type bottles and analyzed for dissolved oxygen, pH, and alkalinity. Dissolved oxygen was measured by the Winkler method, alkalinity was determined by potentiometric titration with 0.05 M H_2SO_4, and pH was measured with a HachOne pH meter utilizing an electrode with a free-flow junction.

Transparency was measured with a 20 cm diameter Secchi Disk.

Water samples for analyses of primary productivity, total phosphorus, phytoplankton, and chlorophyll *a* were collected at selected depths with Van Dorn-type bottles. The phytoplankton primary productivity was measured *in situ* using ^{14}C. Water samples for the analysis of total phosphorus were collected at 0.5 m and were analyzed by the Oregon Department of Environmental Quality Laboratory using Standard Method 4500-PE (APHA 1992). Phytoplankton samples were stored in 250 mL Nalgene bottles and preserved with Lugol's solution (1% of sample volume) until analysis for species composition, density, and biovolume. Chlorophyll *a* samples were filtered in the field and concentrations were measured in the laboratory with a Turner Systems fluorometer.

Zooplankton samples were collected from vertical tows with a 30 cm diameter zooplankton net. Samples were stored in 500 mL Nalgene bottles and preserved with 5% formalin. Zooplankton were enumerated and identified to species, if possible.

Sediment cores were collected from all three lakes using a sling-operated, single piston corer and samples were analyzed for trace metals and diatom remains.

Selected core segments were analyzed for different trace metal fractions or total trace metal concentrations. Sequential fractionation (modified from Tessier et al. 1979), was performed on three depths from two Woahink stations and one Mercer Lake station. Metal concentrations were measured using a Perkin-Elmer Model 305B Atomic Absorption Spectrophotometer attached by an analog-digital converter to a Macintosh 512 computer. Iron, manganese, zinc, copper, cobalt, and nickel absorption were measured in an air-acetylene flame; vanadium was measured using a N_2O-acetylene flame. Matrix effects were corrected for by the standard additions technique.

Total trace metal concentrations were determined by neutron activation analysis. Dried sediment samples from both Woahink stations and Munsel were irradiated in the Oregon State University Triga Reactor and concentrations were measured with a Ge(Li) gamma ray detector. This procedure produced values for total manganese, vanadium, aluminum, iron, cobalt, and arsenic.

Core samples were also analyzed for diatom remains. Dried sediments (10 to 25 mm^3) were processed according to the method of Ven Der Werff (1953). The supernatant was poured into a Batterbee settling chamber and dried onto cover slips. The mounted coverslips were enumerated and identified at 1000x magnification. Direct counts to species were made for a minimum of 300 frustules.

Results and Discussion

Overview

The study lakes share several features in common. Mercer, Munsel, and Woahink are warm monomictic lakes which are common in temperate latitudes near the ocean and are characterized by water temperatures greater than 4° C, free circulation of water during the winter, and summer stratification (Wetzel 1983).

Each of the lakes is thermally stratified from early June through late September. Dissolved oxygen and temperature profiles measured in 1991 and 1992 revealed oxygen deficits in the hypolimnion of each lake, indicative of biologically productive conditions. The 1991 and 1992 profiles were nearly identical to those measured by Griffiths and Yeoman (1938). Phytoplankton are likely responsible for an oxygen maximum that is observed seasonally in the metalimnion of Munsel Lake. Such a maximum occurs when the oxygen created by photosynthesis is trapped by hydrostatic pressure in this transitional layer of water (Wetzel 1983).

The 1938 to 1993 limnological database is spotty, with decades often separating the sampling

periods, making it difficult to assess water quality trends and allowing only qualitative comparisons of earlier and later data. Chlorophyll *a*, total phosphorus, and Secchi Disk depth data for all three lakes show no obvious trends (Daggett 1994). Two exceptions, increased chlorophyll *a* concentrations in Mercer Lake and increased Secchi Disk depths in Woahink Lake, are discussed in subsequent sections about each lake. The lack of vertical differentiation in total manganese, cobalt, and vanadium in sediments of Munsel Lake suggests that this lake has not been extensively impacted by human use (Vogel 1994).

Although not related to eutrophication, a significant finding is the confirmed presence of the predatory zooplankter *Neomysis mercedis* in Munsel and Woahink Lakes. This zooplankter is a relatively large epibenthic crustacean of the order Mysidacea (commonly called mysid or opossum shrimp) which typically migrates into the water column only at night to hunt (Pennak 1989). *N. mercedis* was collected in zooplankton tows made in Munsel and Woahink Lakes during August and September 1991. Pennak (1989) states that introductions of *Mysis* shrimp (a related species in northern and midwestern lakes that fills the same ecological niche as *Neomysis*) have caused "drastic decreases in densities of *Daphnia* and *Bosmina*, as well as shifts in density ratios of other cladoceran zooplankters (p. 460)." In Woahink, predation by *N. mercedis* may be responsible for the apparent extinction of Daphnids, as was observed in Lake Tahoe by Threlkeld (1981) and for the lower than predicted number of pelagic crustacean zooplankton, based on Dodson's (1992) model (observed 6, predicted 10).

Mercer Lake

Data for primary productivity, chlorophyll *a*, iron, and sedimentary diatom remains show evidence of increased biological productivity. The single 1991 ^{14}C primary productivity value was 1.7 times higher than the highest of 13 values recorded from 1970 to 1972 (Table 3). Concentrations of chlorophyll *a* for 1991 and 1992 were two to five times higher than values for similar dates in 1971 (Table 4), except for values measured in late June 1971 that were the highest ever measured in the lake. The increases in relative numbers of *F. Construens* and in organically-associated Fe with decreasing sediment depth also indicate that the lake has become more eutrophic over time (Table 5).

TABLE 3. Phytoplankton primary productivity (mg C m^{-2} h^{-1}).

Mercer Lake	Jul.-Sep. 1970	Feb.-Jan. 1971-1972	Sep. 1991
n	2	11	1
Mean	63.0	28.1	
Maximum	87.0	47.0	146.1(1)
Minimum	39.0	4.0	
Munsel Lake	**Jul.-Sept. 1970**	**Feb.-Jan 1971-1972**	**Aug.-Sep. 1971**
n	2	11	2
Mean	36.0	28.0	80.5
Maximum	40.0	45.0	97.4(3)
Minimum	32.0	8.0	63.5(2)
Woahink Lake	**Jun.-Dec. 1968**	**Feb.-Sep. 1969**	**Aug.-Sep. 1991**
n	8	9	2
Mean	19.91	21.01	65.39
Maximum	37.05	45.96	81.97(5)
Minimum	1.98	2.50	48.80(4)

Note: (1) September 13, (2) August 7, (3) September 3, (4) August 5, (5) September 4

TABLE 4. Comparison of chlorophyll *a* concentrations (µg L^{-1}) in Mercer Lake for selected dates in 1971 and 1991-1992.

Depth (m)	29-Jun 1971	24-Jun 1992	03-Aug 1971	29-Jul 1992	07-Sep 1971	13-Sep 1991
0-3	3.0	5.3	1.5	4.3	3.0	16.3
4-7	7.0	7.0			4.0	11.5
8-9	27.0	8.9	4.5	17.2		
10	5.0		12.0	17.5	13.0	24.4

TABLE 5. Organic iron concentration and percentage of *Fragilaria construens* frustules in Mercer Lake sediments.

sediment depth (cm)	organic iron (mg L^{-1})	*Fragilaria construens* (% of all diatoms)
2	85 ± 55	9.4 ± 6.2
5	80 ± 59	2.8 ± 2.9
20	66 ± 50	1.7 ± 1.6

Evaluation of data for dissolved oxygen, redox potential, conductivity, alkalinity, and nutrients indicates that nutrients are recycled from the sediment of Mercer Lake. In 1991, the following conditions were observed in the hypolimnion:

anoxia, the odor of hydrogen sulfide from water samples, a decrease in redox potential (63 mv to -171 mv) and an increase in conductivity (84 S cm^{-1} to 150 S cm^{-1}) with increasing depth, and a doubling of the alkalinity concentration in the hypolimnion compared to the epilimnion (32.4 mg L^{-1} $CaCO_3$ to 14.7 mg L^{-1} $CaCO_3$). Kavanagh's (1973) data show that the hypolimnetic nitrate concentrations decreased to 0.0 mg L^{-1} during stratification in 1971. Bryant's (1979) data show that hypolimnetic total phosphorus concentrations were two to seven times higher than surface total phosphorus concentrations during the summer of 1978. All of these data are indicative of strong reducing conditions, confirmed by the 1991 redox data, under which nutrients can be mobilized from the sediments. Under these conditions, nitrate is reduced to ammonia, adsorbed phosphate is released from the sediment, and, if sufficient amounts of iron sulfide are precipitated, the accumulated hypolimnetic phosphate may remain in solution during fall turnover (Wetzel 1983). This recycling of nutrients from the sediment is likely the greatest factor contributing to the lake's high productivity.

Munsel Lake

Munsel Lake characteristics were stable over time except for phytoplankton primary productivity. The 1991 primary productivity measurements averaged 1.8 times larger than the maximum value measured from 1970 to 1972 (Table 2).

Although not as pronounced as in Mercer Lake, the 1991 data confirm that since 1938, reducing conditions have existed at the sediment-water interface during stratification, likely causing the release of nutrients from the sediment. This finding is supported by the vertical distribution of total sedimentary iron (Figure 1).

The near-surface increase in total iron in the Munsel Lake sediments is probably a result of natural causes rather than direct anthropogenic effects. Ground waters of the Florence aquifer are both low in dissolved oxygen and high in dissolved iron (Cooper Consultants 1985) and Munsel apparently has a relatively high rate of ground water seepage (Johnson et al. 1985). The dissolved iron is quickly precipitated out when the lake becomes oxygenated to the bottom. Also, the iron dissolved in the deeper anoxic sediments precipitates in the surface zone when it diffuses up into contact with oxygenated hypolimnetic or surficial pore waters (Morfett et al. 1988).

Woahink Lake

Increases in the rate of phytoplankton primary productivity, densities of selected zooplankton species, sedimentation rate, sedimentary vanadium, and numbers of *Cyclotella stelligera* frustules all indicate that Woahink Lake has undergone significant change relative to its presettlement condition. The primary productivity measurements made in 1992 average 1.5 times larger than the maximum rates measured during 1970-1972 (Table 2). A comparison of data from 1991 and Malick (1971) for the total density of four zooplankton species (*Diaphanosoma brachyurum, Diaptomus hesperus, Epischura nevadensis, and Cyclops vernalis)* showed that the lowest 1991 density (15,300 m^{-3}) was almost twice as large as the highest 1968-1969 density (8,200 m^{-3}).

Increased sedimentary vanadium is considered to be a marker of increased human activity because very high concentrations of vanadium are found in petroleum (Charles and Norton 1986). When oil or other fuels are burned, the vanadium present forms V_2O_5 which is highly soluble in water (Lee 1983). Consequently, petroleum combustion is regarded as the primary source of V in freshwater (Charles and Norton 1986).

The increase in vanadium relative to aluminum beginning at 4 cm is probably associated with increased automobile travel along Highway 101 after World War II. Since the lake is immediately east of the highway at the south end of the lake and the prevailing winds blow across the lake (from the southwest during the winter and the northwest to west during the summer), Woahink should have an especially clear record of such an increase. The V:Al increase yields an estimated current sedimentation rate of 1.0 mm per year. This estimate was confirmed by the presence of a zone of decreased V concentration (Figure 2). This decrease in V and three other metals (Vogel 1994) is apparently related to the development of the state park and the Columbus Day wind storm of 1962. The storm and park development deposited trace metal deficient quartz sand in the lake and this appears as a decrease in V concentration at the 1-10 cm sediment depth.

However, the increase in V beginning at 10 cm in the mid-lake cores was not due to increased

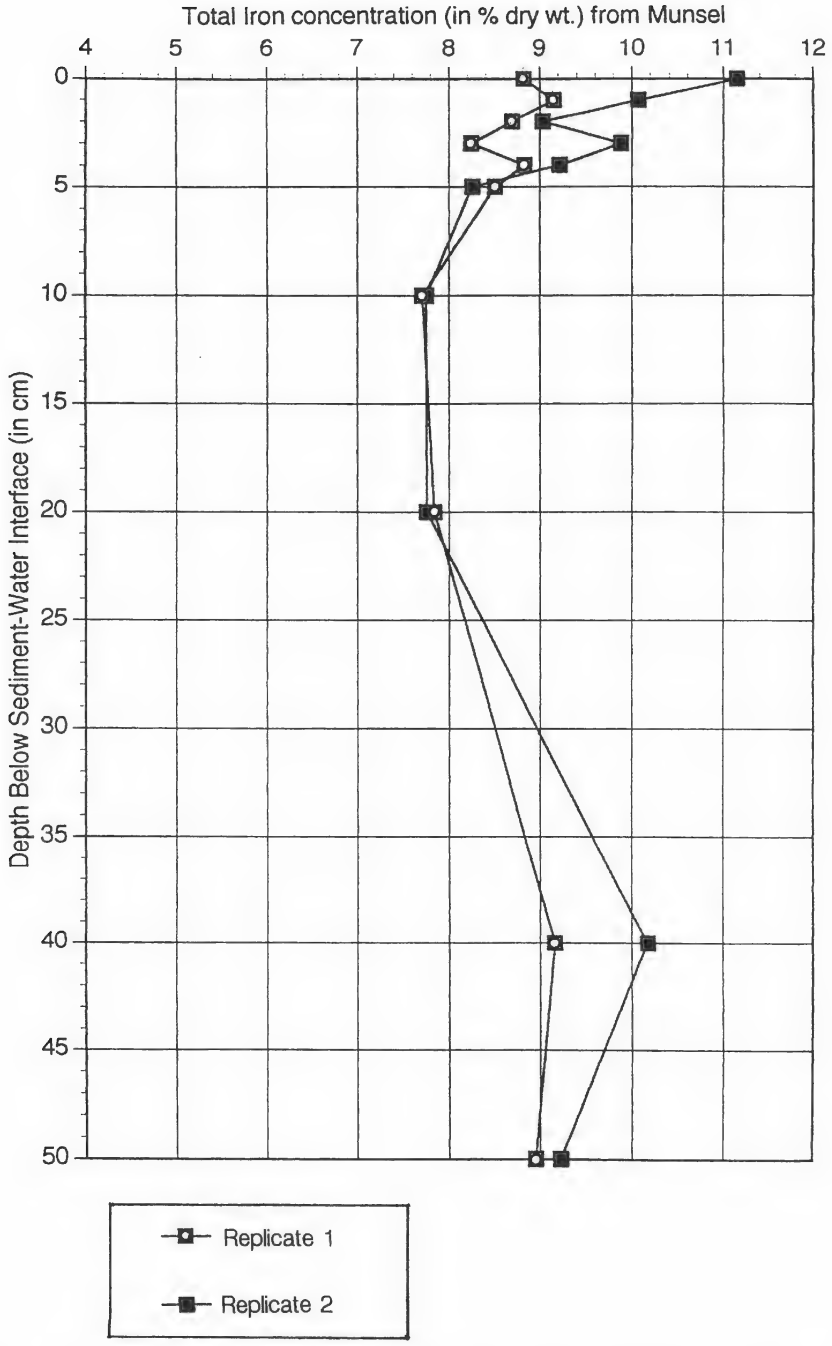

Figure 1. Total iron concentrations in Munsel Lake sediments from replicate cores taken at the deepest point of the lake.

petroleum combustion because the V:Al ratio remained the same, indicating increased erosion as the cause. Increased erosion rates are primarily responsible for increases in sedimentary aluminum concentrations, acid precipitation being the other major cause (Bormann and Likens 1979). The increase in total V apparently marks the onset of deforestation in the Woahink watershed. If it is assumed that the increase began about 1860 when the earliest European-American settlers came to the Florence area, then the sedimentation rate during the homesteading period through the first half of this century was about 0.7 mm per year.

According to Lewis and Pearl Campbell of the Siuslaw Pioneer Museum (1994 personal communication), lakeshore home building greatly increased during the late 1950's and early 1960's. Also, there have been several land developments near the shore, including the state park, that left large areas of bare ground adjacent to the lake (Johnson et al. 1985). This activity probably caused the observed increase in sedimentation rates.

The presence of *Cyclotella stelligera* in Woahink was cited by Johnson et al. (1985) as partial justification for assigning the lake to oligotrophy, yet the relative numbers of frustules from this species, already the most abundant taxon in Woahink sediments, increased by over a third between the lower strata and the 2 cm depth (17.9% $\pm$ 2.3% versus 25.3% $\pm$ 0.0%), the same period of time that the lake has been apparently undergoing cultural eutrophication. The increase in the relative abundance of *C. stelligera* as this lake underwent enrichment may be an early indication of eutrophication. Vogel (1994) noted the correlation between increased vanadium concentration and *C. stelligera* in more recent sediment. Therefore, the recent increased relative sedimentary abundance of *C. stelligera* (and hence, probably the size of its blooms in the water column over time) is likely a result of increased erosion and nutrient loading to Woahink Lake, along with some apparent air pollution, as indicated by the V profile (Figure 2).

Data for chlorophyll *a* and dissolved oxygen show no apparent change over time (Daggett 1994) suggesting that there was a greater shift in species composition than in total primary productivity. There is no evidence of changes in redox conditions over time as demonstrated by the relatively constant vertical sedimentary iron profile (Vogel 1994).

Data for Secchi Disk depth showed an overall increase in water transparency, although it has increased and decreased periodically since 1947 (Figure 3). Secchi depth measurements from 1968 to 1972 are generally greater than measurements made in 1947 but less than measurements made during 1992 and 1993. It is possible that the recent increased transparency results from a shift in phytoplankton species to a community dominated (based on biovolume) by *Gymnodinium* sp., a large spherical dinoflagellate. A community dominated by fewer larger cells would attenuate relatively less light than one composed of more numerous but smaller cells.

Current Trophic State

The estimates of the current trophic states of the study lakes are based primarily on comparison of data from 1991 and 1992 with values compiled by Wetzel (1983) and Sweet (1986), with supporting evidence from the sediment cores. Mercer Lake is mesotrophic to eutrophic, Munsel Lake is mesotrophic, and Woahink Lake is oligotrophic. Except for the concentrations of organic V and Mn in the sediments, the relative amounts of organic trace metals are consistent with the trophic status indices of Mercer and Woahink Lakes (Vogel 1994).

Conclusion

While the results of our investigations are mixed, there have been clear increases in trophic status for each of the lakes. Munsel demonstrated the smallest amount of change, as evidenced by having a change only in primary productivity. The Mercer Lake results indicate a historically mesotrophic lake that has become somewhat more eutrophic. Because Woahink is the most oligotrophic of the three lakes, its relative amount of change was greater, and represents a more significant occurrence.

At Woahink Lake, eutrophication is demonstrated by increased phytoplankton primary productivity, zooplankton population densities, and rate of sedimentation. Evidence of another alteration is the increase in sedimentary vanadium concentration, resulting from increased sedimentation and combustion of petroleum products, and the apparently associated changes in the sedimentary remains of the diatom assemblages. A third major recent biological change is the loss of

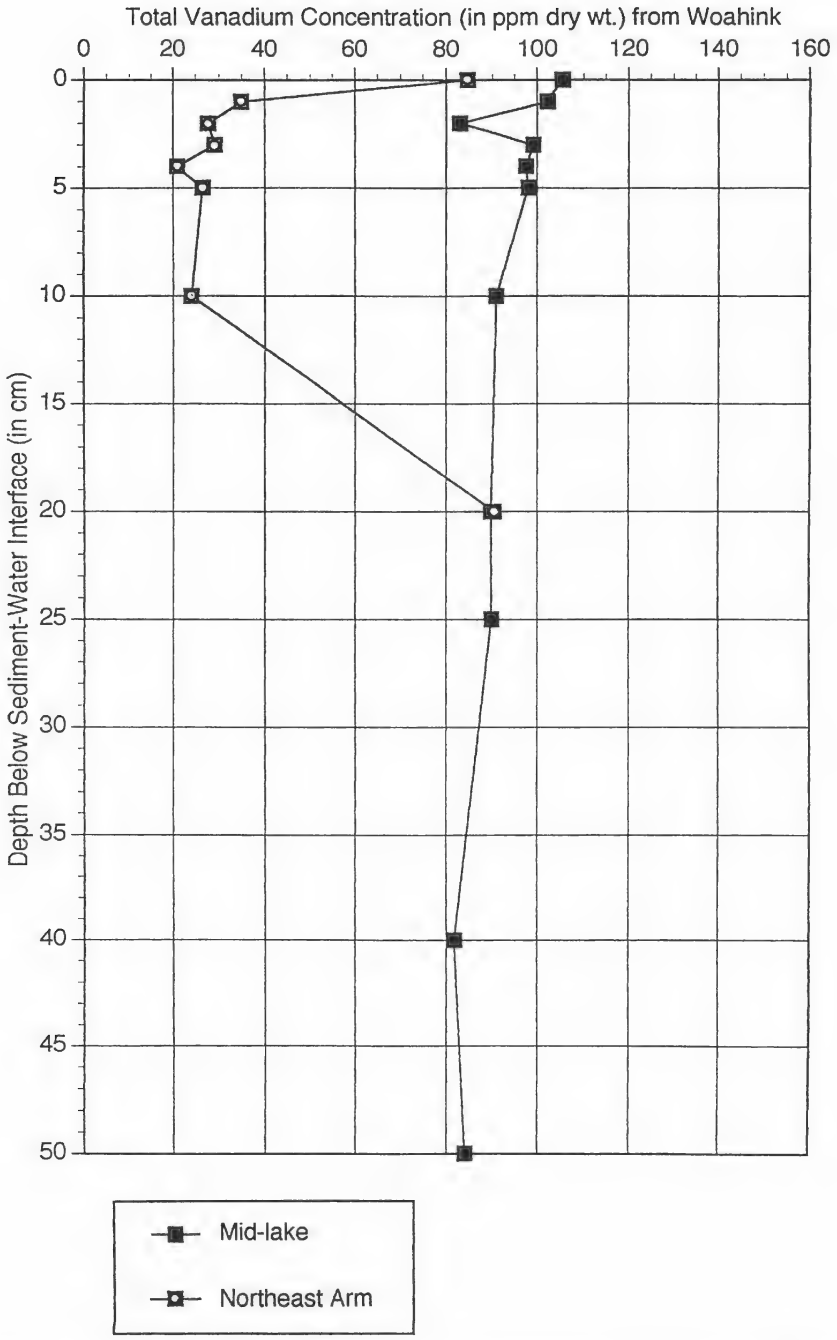

Figure 2. Vanadium concentrations in Woahink Lake sediments from cores taken at the deepest point of the lake and in the northeast arm.

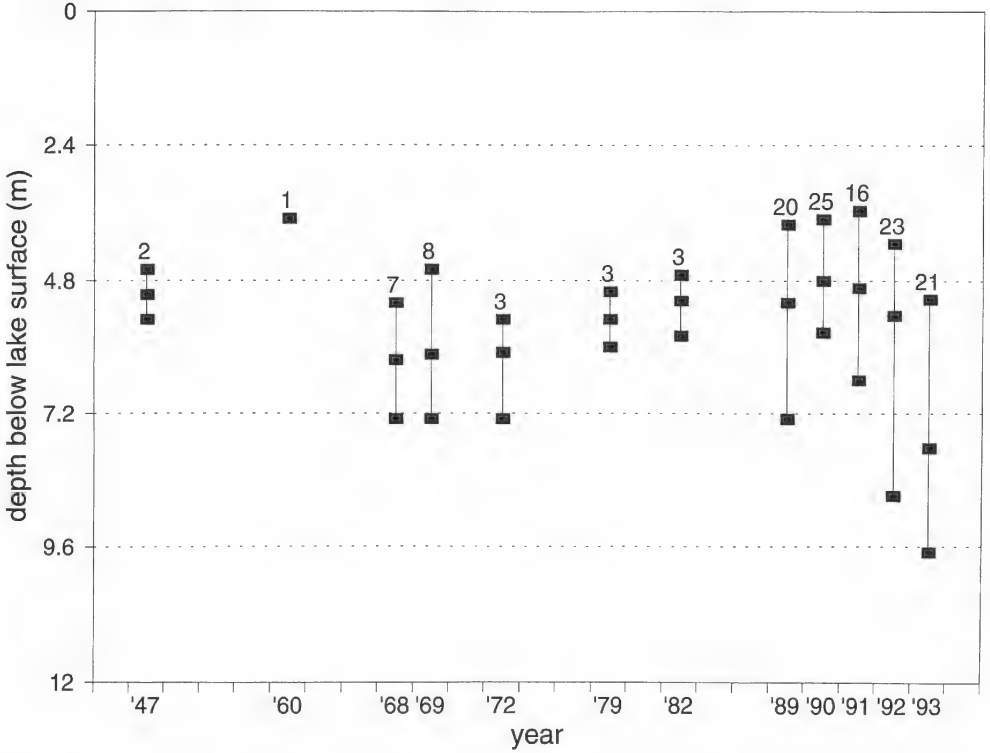

Figure 3. Secchi Disk depths in Woahink Lake (maximum, minimum, and mean; number of measurements above bar).

daphnids probably associated with increases in the *Neomysis* population.

Our findings demonstrate the utility of using multiple parameters to assess possible changes in lake conditions. Although much limnological data was gathered from the lakes between 1938 and 1992, most is not appropriate for assessing trends in lake water quality. This underscores the fact that detection of lake eutrophication and trends in water quality require the systematic collection of appropriate data over long periods of time using methodologies that facilitate statistical analyses or by taking more detailed paleolimnological measurements. While Secchi Disk depth is a cheap reliable indicator of water transparency, sole reliance on it as a method of collecting water quality trend data would not identify significant eutrophication below some threshold level as, for example, in Woahink Lake.

Acknowledgements

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Overview of the Limnology of Crater Lake

Abstract

Crater Lake occupies the collapsed caldera of volcanic Mount Mazama in Crater Lake National Park, Oregon. It is the deepest lake (589 m) in the United States and the 7th deepest lake in the world. The water column mixes to a depth of about 200 m in winter and spring from wind energy and cooling. The deep lake is mixed in winter and early spring each year when relatively cold water near the surface sinks and exchanges positions with water in the deep basins of the lake. The lake becomes thermally stratified in summer and early fall. The metalimnion extends to a depth of about 100 m; thus most of the water column is a cold hypolimnion. Secchi disk clarity measurements typically are in the upper-20-m range to the low-30-m range in summer and early fall. Concentrations of nutrients are low, although conductivity is relatively high owing to the inflow of hydrothermal fluids. Total chlorophyll is low in concentration, but typically maximal at a depth of 120 m during periods of thermal stratification. Primary production also is low, with the maximum levels occurring between the depth of 40 and 80 m. Phytoplankton taxa are spatially segregated from each other within the water column to a depth of 200 m in summer and early fall. The same generalization applies to the zooplankton taxa. Water level, clarity, concentrations of total chlorophyll, primary production, and abundances of zooplankton and introduced kokanee salmon exhibit long-term fluctuations. Based primarily on a recent 10-year study of the lake, the lake is considered to be pristine, except for the consequences of fish introductions.

Introduction

Crater Lake is located in Crater Lake National Park in the southern Cascade Mountains of Oregon, USA. It is the deepest lake in the United States and the 7th deepest lake in the world (Hutchinson 1957). The lake basin (caldera) was formed by catastrophic collapse of the sides of Mount Mazama following a violent eruption about 6,800 years ago (Bacon and Lanphere 1990). The present caldera has steep walls and is between 8 and 10 km in diameter. The lake occupies 78% of its own drainage basin. Crater Lake is the deepest caldera lake in the world, as well as one of the highest in elevation and largest in surface area (Larson 1989; Table 1). No surface outlet exists, but over 40 permanent and ephemeral inlet streams drain into the lake.

The objective of this paper is to summarize the general limnological characteristics of the pelagic zone of Crater Lake, based on unpublished studies conducted between 1983 and 1992 (Larson et al. 1993) or as otherwise cited. Copies of unpublished reports may be obtained from the author. Measurements occurred primarily in the deepest basin of the lake at a site designated as Station 13 (Fig. 1).

TABLE 1. Morphometric characteristics of Crater Lake.

Morphological Attribute	Characteristic	Reference
Bench mark surface elevation	1882 m	Byrne 1965
Surface area	53.2 km^2	Phillips 1968
Maximum depth	589 m	Byrne 1965
Mean depth	325 m	Byrne 1965
Shoreline length	31 km	Byrne 1965

Lake Characteristics

Lake Level

Lake level has exhibited considerable long-term variation since the late 1890's. From 1910 to 1942 the lake dropped about 4 m in elevation, but returned to the 1910 level by the late 1950's. The lake fluctuated by 1 m above and below the bench mark level of 1882 m from 1958 to 1985. Between 1986 and 1994, the level dropped to about 3.5 m below the long-term bench mark elevation.

Water Temperature

The surface of Crater Lake seldom freezes over, owing to the heat content of the massive lake volume and wind mixing. The only known occurrences of ice and snow cover occurred in 1948 and 1985. In 1986 the lake was nearly covered by ice at various times in January and March.

In winter and spring the water mass in Crater Lake circulates to a depth of between 200 and 250 m by wind action and cooling. The deep lake is mixed in winter and early spring each year when

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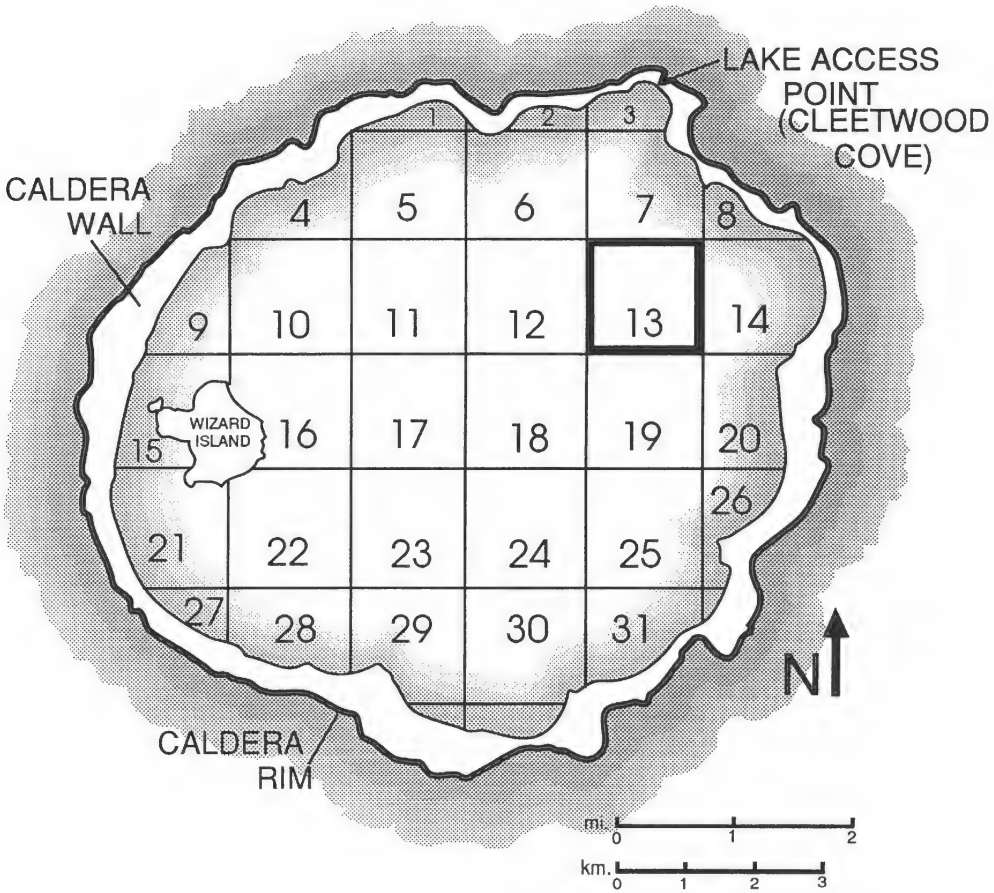

Figure 1. Grid system of Crater Lake stations established by Hoffman (1969). The main monitoring station (13) is 589 m deep.

relatively cold water near the surface sinks and exchanges positions with water in the deep basins of the lake (McManus et al. 1993). In late spring or early summer the temperature of the lake near the surface increases and a thermocline forms between July and September. The depth of the epilimnion is between 5 m and 20 m and is usually deepest in fall because of cooler air temperatures and an increase in mixing generated by storms. Maximum near-surface temperatures ranged from 14.6 to 19.2°C from June or early July to mid-September from 1982 through 1990 (Larson, et al., in press). The metalimnion extends to a depth of about 100 m; thus, most of the water volume is a cold hypolimnion. Annually water temperatures do not vary by more than 1°C below a depth of 100 m. The temperature at the bottom of the water column is about 3.5°C (Larson et al., in press).

Water Chemistry

The average pH of the entire water column of Crater lake is 7.5. Average near-surface pH ranges from about 7.6 to 7.7, whereas the pH decreases with increased lake depth and is about 7.3 at a depth of 550 m. The average total alkalinity and specific conductance are 27 mg/l and 115 µmhos/cm, respectively. Both variables increase slightly with increasing lake depth. The average concentration

of dissolved oxygen is relatively uniform in the water column in spring, but decreases to about 90% saturation at 550 m during the period of thermal stratification. Nitrate-nitrogen, ammonia-nitrogen, Kjeldahl-nitrogen, total phosphorus and orthophosphate-phosphorus occur in low concentrations (Table 2). Nitrate-nitrogen is virtually undetectable in the upper 200 m of the water column; however, the concentration increases to maximum with increased depth. Kjeldahl-nitrogen and ammonia-nitrogen decrease in concentration with increased lake depth, whereas orthophosphate-phosphorus increases. Total phosphorus is nearly uniform in concentration throughout the water column (Larson et al., in press).

TABLE 2. Mean concentrations of selected chemical variables for all samples obtained from the indicated depth intervals in Crater Lake, 1982-1990.

	Depth Interval (meters)		
Variable	0-200	200-550	0-550
Nitrate-N (µg/l)	0.61	10.62	6.98
Ammonia-N (µg/l)	2.55	2.34	2.41
Kjeldahl-N (µg/l)	18.52	11.55	14.08
Orthophosphate-P (µg/l)	12.21	13.88	13.27
Total phosphorus (µg/l)	28.22	29.59	29.09

Secchi Disk Clarity and Depth of 1 Per Cent Incident Light

During the period from 1982 to 1992, water clarity measurements obtained with a Secchi disk generally fluctuated between readings in the upper-20-m range to the low-30-m range from June to September. The deepest reading recorded since 1969 was 40.8 m in August 1994; the shallowest August reading of 22.9 occurred in 1991 (Larson et al., in press). Secchi disk clarity was shallow in late winter and early spring, apparently in relation to input of particles from avalanches and snow-melt. Clarity typically increased in June and early July, and then declined in August when the lake was thermally stratified and then increased in fall; in some years reduced clarity in fall has been associated with storms (Larson et al., in press).

The depth of 1 per cent of the incident sunlight penetrating the surface of the lake, measured by a photometer with a white filter, illustrates the great clarity of the lake. In July the 1 per cent depth ranged between 90.3 and 99.5 m between 1986 and 1989, whereas in August, the 1 per cent depth ranged between 86.1 and 103.4 m (Larson et al., in press).

Phytoplankton

During the period from 1983 to 1990, a total of 157 phytoplankton taxa were identified, including 55 diatoms, 53 chrysophytes, 1 xanthophyte, 21 chlorophytes, 12 dinoflagellates, 6 cryptomonads, 7 cyanobacteria, and 2 unknown taxa. In winter the flora was uniformly distributed to the depth of mixing. *Stephanodiscus hantzschii*, *Ankistrodesmus spiralis,* and a small unidentified chrysophyte were the dominate taxa during this period of the year. During the period of thermal stratification, phytoplankton are spatially segregated within the water column to a depth of 200 m. *Nitzschia gracilis* was the dominant taxa in the upper 40 m of the water column. *Ankistrodesmus spiralis*, *Dinobryon sertularia*, *Tribonema* sp., *Rhodamonas lacustris* and *Gymnodinium inversum* were the dominant taxa from 60 to 100 m. From 120 to 200 m the dominant taxa were the same as during winter (McIntire et al., in press).

Concentrations of total chlorophyll were maximum usually at 120 m during periods of thermal stratification from 1984 to 1990. Peak concentrations of total chlorophyll were always less than 2 µg/l however. Total chlorophyll integrated to a depth of 200 m exhibited cyclic changes between 1979 to 1990. For example, peak concentrations in August occurred in 1980 (120 mg/m^2) and 1986 and 1987 (100 mg/m^2). Primary production was low between 1986 and 1990, using the carbon-14 assimilation method. Maximum primary production occurred between 40 and 80 m during periods of thermal stratification from 1986 to 1990, although relatively high production values occasionally were observed in near-surface samples (McIntire et al., in press). Primary production in August exhibited a similar cyclic pattern as did total chlorophyll. Between 1980 and 1990, peak assimilations in August integrated to a depth of 180 m occurred in 1980 (30 mg C/m^2/hr) and 1987 (58 mg C/m^2/hr).

Zooplankton

During the period from 1985 to 1990, two crustacean taxa and 11 rotifer taxa were collected in Crater Lake (Table 3). In winter, most of the taxa

were distributed from the lake surface to the depth of mixing (200-250 m). During periods of thermal stratification the taxa were spatially segregated within the water column. *Polyarthra* was the dominant taxon in the upper 40 m of the lake, but it occurred in low density. Between 40 m and 80 the dominant taxa were *Bosmina*, *Polyarthra*, *Kellicottia* and *Asplanchna*. From 80 to 120 m the dominant taxa were *Daphnia*, *Keratella*, *Synchaeta*, *Filinia* and *Polyarthra*. The dominant taxa from 120 to 200 m were *Philodina*, *Conochilus*, *Keratella* and *Collotheca* (Larson et al., in press).

Some taxa were not present every year from 1985 to 1990. *Philodina* was present between 1985 and 1988, *Conochilus* was present in 1985, and *Asplanchna* was present in 1990. *Daphnia* was not present in quantitative subsamples in 1985, and was in low density in 1986. The population reached its maximum abundance in 1988, declined to low density by 1990, and was absent in 1993 (Robert Truitt, personal communication).

TABLE 3. Zooplankton species found in samples from Crater Lake, 1985-1990.

Phylum or Order	Taxon
Cladocera	*Daphnia pulicaria (Forbs) (emend. Hrbacek)*
	Bosmina longirostris (sensu latu)
Rotifera	*Keratella cochlearis (Gosse) morph macracantha (Lauterborn)*
	Keratella quadrata var. dispersa (Carlin)
	Kellicottia longispina (Kellicott)
	Polyarthra dolichoptera (Idelson)
	Philodina cf. acuticornis (Murray)
	Filinia terminalis (Plate)
	Synchaeta oblonga (Ehrenberg)
	Synchaeta lakowitziana (Lucks)
	Conochilus unicornis (Rousselet)
	Collotheca pelagica (Rousselet)
	Asplanchna sp.

Fish

Crater Lake was naturally barren of fish. Several salmonid species were introduced into the lake between 1888 and 1941. Kokanee salmon and rainbow trout were the only species of fish collected from the lake between 1986 and 1994. Kokanee salmon were cyclic in abundance. Rainbow trout appeared to be less cyclic in abundance than were kokanee salmon.

Kokanee salmon primarily live in the pelagic zone of the lake from the surface to a depth of about 100 m. They prey on small emerging benthic macroinvertebrate pupae and larvae and terrestrial insects landing on the lake surface. They also prey on *Daphnia*. Rainbow trout live in the nearshore area of the lake. They prey on large bodied terrestrial insects from the lake surface and benthic macroinvertebrates. Rainbow trout also prey on kokanee salmon.

Discussion

Crater Lake is a dynamic and complex system as illustrated by long-term fluctuations of water level, clarity, chlorophyll, primary production, zooplankton and kokanee salmon, and the spatial segregation of the water column by phytoplankton and zooplankton. Long-term changes in lake level results from shifts in the water budget. Changes in the amount of chlorophyll and primary production appear to be related to deep-water mixing of the water column during winter and spring. This upwelling phenomenon moves nutrient-rich waters in the deep lake to the upper 200 to 250 m of the water column (McManus et al. 1993). *Daphnia* abundances appear linked with periods of increased primary productivity; however, predation by kokanee salmon probably impacts their abundance and may be the reason for its reduced abundance in 1990 and disappearance in quantitative samples by 1993.

Chemical and physical properties of Crater Lake that are most consistent with typical oligotrophic characteristics of lakes include high transparency, an orthograde nitrate-N depth profile, and low concentrations of nitrate-N in the epilimnion. Specific conductance in Crater Lake often exceeds those of eutrophic, mesotrophic and oligotrophic lakes in the Cascade Mountains of Oregon (Table 4). The relatively high conductivities of Crater Lake and the other two caldera lakes included in Table 3 (East Lake and Paulina Lake) are associated with inputs from hydrothermal fluids. In comparison to the range of conductivities of caldera lakes worldwide, however, the conductivities of caldera lakes in Oregon are low (Larson 1989). Furthermore, the relatively high concentrations

TABLE 4. Concentrations of selected chemical variables in water samples from near surface waters of eutrophic (E), mesotrophic (M), and oligotrophic (O) lakes in the Cascade Mountains of Oregon. Data for the State of Oregon were obtained from Johnson et al. (1985).

Lake	Class	Elevation (m)	Area (ha)	Depth (m)	Alkalinity (mg/l)	Cond (µmhos/cm)	pH	T-Phos (µg/l)
Diamond	E	1579.8	1300.7	15.8	15	29	9.5	61
Suttle	E	1047.9	102.4	22.9	15	50	8.4	24
East	M	1941.6	422.5	54.9	103	310	7.9	16
Gold	M	1467.0	38.9	13.1	16	33	7.3	47
Marion	M	1258.8	105.6	56.4	18	37	8.8	33
Odell	M	1459.1	1449.6	86.0	13	32	9.3	28
Paulina	M	1929.7	619.6	76.2	340	560	8.3	45
Big	O	1415.5	76.9	23.5	<1	4	7.2	2
Blue	O	1052.5	21.9	95.7	16	50	6.9	29
Breitenbush	O	1676.4	26.3	7.6	<1	6	7.6	—
Charlton	O	1734.9	63.1	29.0	2	6	6.8	4
Crescent	O	1474.9	1840.2	80.8	11	26	7.6	62
Deer	O	1492.3	21.0	7.9	3	12	6.5	17
Devils	O	1658.1	9.3	3.0	10	25	—	72
Doris	O	1618.5	27.9	29.0	<1	4	—	3
Hariette	O	2057.4	16.2	24.1	<1	3	—	9
Lost	O	958.0	93.5	53.3	2	12	6.6	6
Olallie	O	1504.5	76.1	13.1	<1	3	—	8
Summit	O	1692.6	195.1	19.2	<1	6	6.7	9
Waldo	O	1650.2	2848.8	128.0	<1	3	6.3	9
Crater	O	1882.4	5317.4	589.0	40	108	7.2	17
Crater[1]	O	1882.4	5317.4	589.0	26-30	80-121	7.1-7.9	13-43

[1]Data from 0 to 550 m, 1983-1990 (Larson et al. In press).

of total phosphorus in Crater lake is in the range usually associated with mesotrophic lakes (Wetzel 1983). Therefore, some of the chemical properties of Crater lake do not conform to the entire range of criteria usually associated with oligotrophic status.

Limnological studies of Crater Lake conducted by the National Park Service between 1982 and 1992 were in response to an apparent decline in lake clarity. Congress passed Public Law 97-250 in the fall of 1982, which authorized and directed the Secretary of the Interior to conduct a 10-year limnological study of the lake. At the end of the study, researchers concluded that Crater Lake was pristine except for the consequences of introduced fish. Although fish affected the food web of the lake, no other changes caused by human activities specifically could be identified or separated from those caused by natural phenomena.

Results of the limnological study of Crater Lake between 1982 and 1992 revealed many of the components and processes important to lake clarity and to the dynamics of the lake ecosystem as a whole (Table 5). Although the relative importance of these components and processes was well documented in many instances, the level of knowledge of them was generally low to moderate because they could not be addressed in sufficient detail within the scope of the program. This shortfall posed a problem because several human-related activities and conditions were identified which may have negative impacts on the lake (Table 6). Although our level of knowledge of the magnitude of the impacts on the lake was low in most cases, suspected contamination of an intra-caldera spring, commonly referred to as Spring 42, from a sewage septic-drainfield on the caldera rim in the vicinity of Station 28 (Fig. 1) received considerable attention during the limnological study because of its potential impact on lake productivity. Results from studies of particle flux in the lake clearly demonstrated that any nitrate contamination in Spring 42 from the sewage system would not have a significant affect on lake clarity and productivity. Nonetheless, as a precautionary measure, park management disconnected the sewage system in 1991 and removed it from the caldera

TABLE 5. A rating of the importance of selected processes or components of the Crater Lake ecosystem in relation to knowledge of lake clarity and the lake system. A rating of the level of knowledge of the processes and components is included (after Larson et al. 1993).

Component or Process	Relative Importance to Understanding Lake Clarity	Relative Importance to Understanding the Lake System	Level of Knowledge
Lake level	Moderate	Moderate-High	Moderate
Water budget	Moderate	High	Moderate
Depth of survace mixing in winter	High	High	Moderate
Thermal stratification	High	High	Moderate
Depth of surface mixing in fall	High	Moderate	Low
Abiotic particles: mudslides, avalanches, runoff & storm events	High	Low-Moderate	Low
Nutrient budget	Moderate	High	Moderate
Hydrothermal inputs	Low	High	Moderate
Organic detritus			
Water column	Moderate	High	Moderate
Benthic	Low	High	Moderate
Nutrient upwelling from the deep lake	High	High	Moderate
Spring 42 nitrate - N	Low	Low	High
Atmospheric deposition			
Nutrients	Moderate	High	Moderate
Particles	?	Low-Moderate	Low
Particle flux	Moderate	High	Moderate
Boat and automobile Emissions/Petroleum wastes	?	?	Low
Phytoplankton production dynamics	Moderate-High	High	Moderate
Zooplankton production dynamics	Low-Moderate	High	Low-Moderate
Benthic flora (production & nutrient dynamics)	Low	High (?)	Low
Benthic fauna (production dynamics)	Low	Moderate	Low
Fish production dynamics	Low-Moderate	High	Low-Moderate

rim in 1992. Sewage from the rim now is piped by gravity to settling ponds on the flanks of Mount Mazama about 300 m in elevation below the caldera rim.

Crater Lake is a unique lake from an international perspective, and it is highly valued both nationally and locally. Responsibility for management of such a system is a priority for the National Park Service. Furthermore, the long-term data set that now exists for the lake has great scientific value for understanding processes that are common to all aquatic systems. Few pristine lake have received such extensive and intensive studies. The National Park Service recognizes that maintaining the pristine conditions of the lake will require regulation of human activities within the context of existing information and regulations, while simultaneously supporting the collection of additional information. Long-term monitoring of selected features of the lake system coupled with special short-term studies are needed for additional information for management and scientific purposes. In 1994, the National Park Service provided funding to continue long-term limnological studies of the lake.

TABLE 6. Activities or conditions that may impact Crater Lake and a rating of the level of understanding of the potential impacts (after Larson et al. 1993).

Issues of Concern	Processes or Components Impacted	Level of Understanding of the Impact
Atmospheric deposition	Nutrients	Moderate
	Particles	Low
Automobile and boat emissions	Carbon particles	Low
	Chemicals	Low
Contamination of Spring 42	Nitrate-N concentration	High
Road and parking lot runoff	Release of petroleum products	Low
Global climate change	Depth of surface mixing	Low
	Amount of deep lake circulation	Low
	Amount of preciptation	Low
	Primary and secondary production	Low
Introduced species:		
Crayfish	Benthic food web	Low
Rainbow trout	Predation on:	
	Benthic macroinvertebrates	Low
	Terrestrial insects	Low
	Amphibians	Low
	Benthic and pelagic food webs	Moderate
Kokanee salmon	Predation on:	
	Benthic macroinvertebrates	Low
	Terrestrial insects	Low
	Daphnia pulicaria	High
	Pelagic food web	Moderate

The long-term limnological monitoring program at Crater Lake will focus on the collection of meaningful information about the status and trends of the lake. The program will provide a minimum set of standards by which the status of the system can be evaluated as well as baseline data needed to support specific investigations into lake processes that we do not fully understand. Understanding those processes that affect lake clarity will be the highest priority of the monitoring program. An array of variables will be monitored (Table 7) following methods developed during the initial study and described in various chapters of the final report from the study (Larson, et al. 1993). The lake will be sampled at monthly intervals between June and September, when the lake is accessible by foot and when boats can be moored on the lake. Although weather conditions in the park are not predictable from year to year, sampling also will be attempted each year in January and April to match the "off-season" sampling conducted during the initial study. January and April samples provide estimates of the amount of deep-water circulation, concentrations of nutrients, primary productivity, and characteristics of the phytoplankton and zooplankton communities. Sampling from June through September provides information on limnological conditions of the lake during the period of thermal stratification. With few exceptions, samples will be taken at Station 13 to be consistent with the major sampling site used in the initial study.

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TABLE 7. Monitoring variables at Crater Lake and at intra-caldera springs of the lake.

Weather
Precipitation, wind speed and direction, termpearture, humidity, and solar radiation

Lake temperature and conductivity
Conductivity, temperature, and depth probe (CTD) from surface to a depth of 550 m.

Optical properties of the lake
20-cm Secchi disk
Photometer (to 150 m)
Transmissometer (to 550 m)

Abiotic properties of the lake

Chemical properties of the lake
Total alkalinity, pH, specific conductance, and concentrations of dissolved oxygen, total phosphorus, orthophosphate-phosphorus, nitrate-nitrogen, total Kjeldahl-nitrogen, ammonia-nitrogen, silica, and trace elements at selected depths from the following depth sequence: 0, 5, 10, 20, 60, 100, 200, 300, 400, 500, and 550 m.

Biological properties of the lake
Chlorophyll *a* concentration
In vitro chlorophyll concentration according to the following depth sequence: 5-m intervals from 0 to 10 m, 20-m intervals from 20 to 200 m, and 25-m intervals from 200 to 300 m, including contribution from picoplankton collected through differential filtering.
C-14 primary production at the chlorophyll sampling depths to 180 m, including contribution from picoplankton collected through differential filtering
Phytoplankton
Species, density, and biovolumes at all chlorophyll sampling depths to a maximum depth of 200 m
Zooplankton
Species, density, and biomass in samples obtained by a vertical tow of a .5 m diameter, number 25 closing net
Fish
Species, abundance, biomass, spatial distribution, age, sex, growth, and food habits. Samples collected with gill nets, hook and line, and down rigger. Pelagic distributions estimated using an echo-sounder.

Bulk atmospheric deposition to the lake

Springs 20, 38, 39, 42, 48
Temperature, pH, conductivity, alkalinity, nutrients, trace elements, and bacteria (total coliform, fecal coliform, and fecal streptococcus).

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Diel Study of Lemolo Lake, Douglas County, Oregon

Abstract

As a component of a program of environmental studies associated with relicensing of the North Umpqua Hydroelectric Project, limnological data were routinely collected in Lemolo Lake, a 419 acre reservoir in Douglas County, Oregon, from 1992-1994. In addition to the periodic data, an intensive, short-term study was conducted to provide information on diel changes in the reservoir during a period of heightened primary production. This paper describes the results of the diel study.

Data collected over a 24-hour period consisted of *in situ* profiles, continuous monitoring, and sample collection in both the reservoir and the North Umpqua River approximately 800 meters downstream of the dam. Data collected in the reservoir were indicative of eutrophic conditions, and nitrogen limitation. Chlorophyll *a* concentrations for samples collected August 11 and 12, 1993 were 28.4 and 33.4 µg/L, respectively; as compared to 1 µg/L in July. Phytoplankton biomass was dominated by the blue-green algae *Anabaena.* Secchi depth was markedly reduced during the study period, and epilimnetic pH remained near 9.0.

This study highlighted the existence of a surface layer in Lemolo Lake which can become highly productive during the summer months. Withdrawal of hypolimnetic water for power generation and instream flow creates lentic conditions on top of a more lotic hypolimnion. Overall retention of the reservoir is short (15 days), but slow growing cyanobacteria and large bodied cladocerans are indicative of longer retention of Lemolo Lake surface waters. The ability to remain buoyant in the water column, and to thrive in a nitrogen poor system, are particularly important advantages for *Anabaena* in Lemolo Lake.

Introduction

Lemolo Lake is a 419 acre reservoir on the North Umpqua River in Douglas County, Oregon. As a component of studies conducted for relicensing of PacifiCorp's North Umpqua Hydroelectric Project, limnological data were collected at Lemolo Lake from June 1992 through November 1994. Sampling was conducted at monthly intervals in 1992 and 1993, and in July and September 1994.

In general, water quality in Lemolo Lake is typical of other mid-elevation Cascade lakes (Rinella 1979, Eilers and Bernert 1990, Landers et al. 1987). Total phosphorus concentrations (June 1992 through September 1994) averaged 36 µg/L P, ortho-phosphorus averaged 25 µg/L P, and inorganic nitrogen (nitrate+nitrite) was generally below detection (less than 50 µg/L N in 1993, and 5 µg/L in 1994). Specific conductance averaged approximately 50 µS/cm. Secchi depth averaged 5.2 meters and turbidity was generally low (average 1 NTU).

In contrast to unproductive conditions during the majority of the year, Lemolo Lake experiences seasonal algal blooms during the late summer or early fall. These blooms, made up of blue-green algae (*Anabaena*), result in markedly reduced Secchi depths, increased turbidity, and significantly higher chlorophyll *a* concentrations. In addition, pronounced diel changes in pH and dissolved oxygen occur during these periods. During blooms in 1992 and 1993, pH exceeded 8.5 from the surface to a depth of several meters, and dissolved oxygen exceeded 120 percent saturation (PacifiCorp 1995).

PacifiCorp conducted an intensive (24 hour) study of Lemolo Lake during August, 1993 to provide more detailed information during a period of heightened primary production. This study included collection and analysis of surface water samples and vertical profile measurements; collection of continuous (half-hourly) data at near surface and hypolimnetic depths; and collection of continuous data at a downstream location in the North Umpqua River. The objective of the study was to document diel changes in Lemolo Lake during an algal bloom, and to assess downstream effects of these conditions on the North Umpqua River.

Site Description

Lemolo Lake (43° 19' N, 122° 12' W) is located within the Umpqua National Forest approximately

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75 miles east of Roseburg, Oregon, and 16 miles north of Crater Lake National Park (Figure 1). In addition to the North Umpqua River, inflows to the reservoir include Lake Creek, the outflow from Diamond Lake; and Poole Creek.

PacifiCorp's 37-meter (120-foot) dam located at RM 93 on the North Umpqua River creates Lemolo Lake. The reservoir inundates about 3 km of the North Umpqua River and 2 km of Lake Creek. Lemolo Lake has a maximum depth of about 30 m at full pool. The reservoir has an average retention time of 15 days (Johnson et al. 1985), which may increase to approximately 20 days during the summer low flow period (PacifiCorp 1995).

At full pool (1,264.5 m [4,148.5 feet] elevation) Lemolo Lake has a volume of approximately 14.5 million m^3 (11,750 acre-feet) and a surface area of 170 ha (419 acres). In 1993, the reservoir was reduced to 828,000 m^3 (670 acre-feet) and 21 ha (51 acres) during the winter drawdown period.

Water can exit Lemolo Lake via 4 routes: (1) the intake to the Lemolo No. 1 waterway; (2) the intake for the instream flow release to the North Umpqua River; (3) high capacity spillway valves at the base of the dam; and (4) the surface spillway of the dam. The intake structures for the waterway, instream flow, and spillway valves draw water from the hypolimnion of the reservoir, at a depth of approximately 18 meters (60 feet) at full pool. With the exception of the Christmas 1964 flood, the surface spillway has not been used since construction of the dam in the mid-1950's.

Lemolo Lake is managed primarily for hydropower, recreation, and flood management. Resident fish species include brown trout (*Salmo trutta*), rainbow trout (*Oncorhyncus mykiss*), kokanee (*Oncorhyncus nerka*), and tui chubs (*Gila bicolor*). All resident fish spawn naturally in the lake or its tributaries; no stocking program currently exists in Lemolo Lake. The U.S. Forest Service maintains three primitive campgrounds on the lake. A privately owned resort on the lake north of Poole Creek includes a small lodge and several cabins.

Climate: The climate of the Lemolo Lake area is typical of a moist, maritime regime with wet, mild winters and dry summers. Average annual precipitation in the North Umpqua Basin (extending from Maidu Lake on the west side of the Cascades to the confluence of the North and South Umpqua Rivers near Roseburg, OR) ranges from 86 cm (34 inches) at lower elevations to 188 cm (74 inches) at higher elevations (Radtke and Edwards 1976). About 80% of the annual precipitation typically falls from October through March. A snow pack generally persists throughout the winter above 900 meters (3,000 feet). Mean annual temperatures range from 12°C in Roseburg to 4°C at Crater Lake.

In contrast to predominantly dry conditions that have existed in the Lemolo Lake area over the last 10 years, precipitation during 1993 (August 31, 1992 through September 30, 1993) was 216 cm (85 inches), 58 cm (23 inches) above average for the period 1966-1994. Record low snowfall was recorded at Lemolo Lake during 1992, and precipitation was significantly below average in both 1992 and 1994 (PacifiCorp records at Lemolo No. 1 weather station).

Geology and Soils: The North Umpqua River lies within the Cascade Mountain Range, a Cenozoic volcanic province. The North Umpqua River has incised canyons through volcanic flows which have weathered in many areas to clay-rich soil and saprolite (Peck et al. 1964). Volcanic eruptions are present in the stratigraphic record from Pliocene to Holocene. Exposures of younger Quaternary glacial till are present in the eastern portion of the basin above 1,200 meters (4,000 feet). This is locally underlain by thick deposits of ash and pumice from the eruption of Mount Mazama, approximately 7,600 years ago. Roadcuts along Highway 138 west of Lemolo Lake reveal these deposits, which are over 15 meters thick in some areas.

Soils in the Lemolo Lake area are derived from volcanic flows. The upper meter of soil is predominantly derived from Mazama ash and pumice (Radtke and Edwards 1976). These soils are moderately to extremely well drained.

Methods

The diel study was conducted on August 11 and 12, 1993. Both days were clear and warm, with no precipitation. Water column profiles of temperature, dissolved oxygen (DO), pH, and specific conductance were measured during the afternoon of each day using a Hydrolab® Surveyor III. Measurements were recorded at 0.5 meter intervals to a depth of five meters, and at one meter intervals from five meters to the reservoir bottom. The Hydrolab® was calibrated prior to use each day.

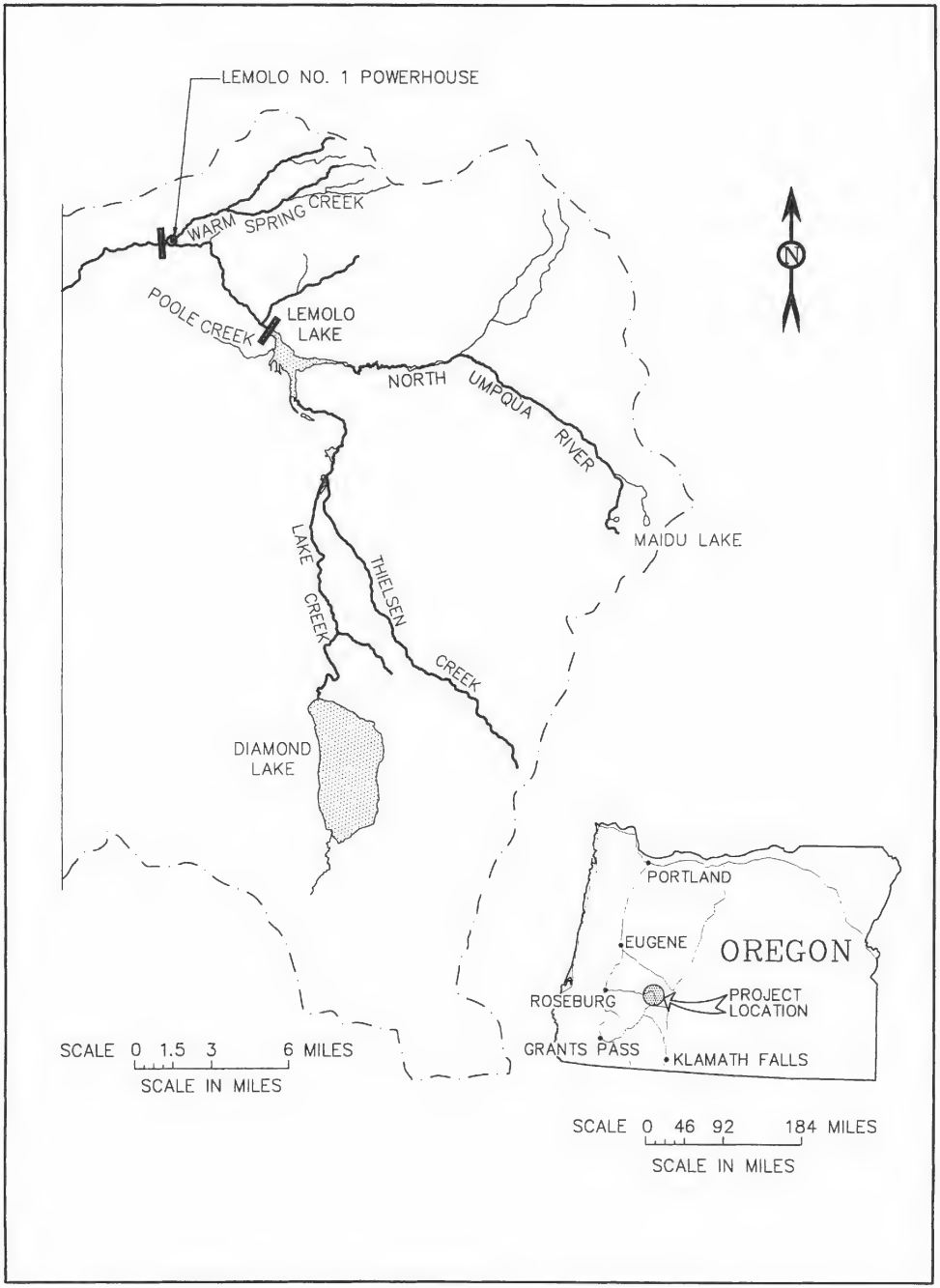

Figure 1. Location of Lemolo Lake, Douglas County, Oregon.

Continuous monitoring of DO, temperature, pH, and specific conductance was conducted in Lemolo Lake and in the North Umpqua River downstream of the dam over a 24-hour period. Reservoir data were recorded every 30 minutes at depths of 2 meters and 15 meters, beginning at 1400 hours on August 11. Continuous monitoring in the North Umpqua River began at 1600 hours on August 11, with the same frequency of measurement. The instream data were collected at the USGS gaging station (Gage No. 14313500), approximately 800 meters downstream of Lemolo Lake dam.

Continuous monitoring data were collected with Hydrolab® Datasonde III units. Instruments monitoring conditions in Lemolo Lake were suspended from an anchored boat. The stored data were downloaded in the field on completion of the study and transferred to PC-compatible data files.

In conjunction with the vertical profiles, surface grab samples were collected for analysis of nutrients and turbidity on both dates. Chlorophyll *a* samples were collected as a composite of three equal volumes from the surface, thermocline, and the midpoint between these depths. Chlorophyll *a* samples were stored in opaque bottles. All samples were iced following collection and transported to the laboratory within 24 hours of collection. U.S. EPA approved or Standard Methods were used for all laboratory analyses.

Additionally, samples for zooplankton and phytoplankton were collected on August 11. Zooplankton samples were collected using a 30 cm diameter, 80 µm mesh plankton net, and preserved in the field with 10% buffered formalin and BHT (butylated hydroxytoluene, a color preservative). The net was towed from near the reservoir bottom to the surface (approximately 18 meters). Phytoplankton samples were collected as surface grab samples and preserved with a 1% Lugol's solution.

All reservoir data and samples were collected at a single location in Lemolo Lake, approximately 1.6 km upstream of the dam off the northern shore. The original North Umpqua River channel exists along this side of the reservoir.

Results

Vertical Profiles

Vertical profiles of temperature, DO, pH, and specific conductance varied little between August 11 and 12 (Figure 2). Strong thermal stratification was apparent on both days of the study, with the thermocline residing at a depth of approximately 3 meters. Temperature ranged from 9°C at the bottom of the reservoir (19 meters) to 18°C at the surface.

Hypolimnetic oxygen concentrations in Lemolo Lake were not substantially depleted. Minimum DO was 9.7 mg/L on August 11, and 9.1 mg/L on August 12. The maximum DO observed was 12.7 mg/L at a depth of 4 meters on August 11. Maximum DO concentrations were measured near the thermocline on each day of the study (Figure 2), presumably due to phytoplankton photosynthesis at this depth.

Measurements of pH ranged from 7.4 to 9.1 on August 11, and from 7.5 to 9.1 on August 12. On both afternoons, pH exceeded 8.5 from the surface to a depth of five meters. The maximum pH was recorded at two meters on each day.

Specific conductance increased slightly with depth. Values ranged from 46 to 51 µS/cm.

Continuous Data Collection

Continuous measurement of temperature, DO, pH, and specific conductance revealed distinct differences between the 2 and 15 meter depths in Lemolo Lake. However, data collected at the 15 meter depth and at the USGS gaging station in the North Umpqua River were quite similar (Figure 3). As previously mentioned, water is released from Lemolo Lake to the North Umpqua River at a depth of approximately 18 meters at full pool elevation. The gaging station is located approximately 800 meters downstream of the Lemolo Lake dam.

Temperatures at 2 meters in Lemolo Lake averaged 17.4°C and ranged from 17.0 to 17.8°C. Average temperature was 8.6°C at 15 meters, and 9.7°C at the USGS gage. A weak diel temperature pattern was evident at the USGS gage (range 9.2 to 10.8°C). Temperatures at 15 meters were essentially constant over the study period (range 8.5 to 8.8°C).

Dissolved oxygen concentrations exhibited strong diel variation, ranging from 9.3 to 12.1 mg/L at two meters, and from 8.8 to 11.1 mg/L at 15 meters. Maximum oxygen concentrations at two meters occurred during the afternoon of August 12, reaching 127% of saturation at 1400 hours. Minimum DO at two meters was 96% of saturation at 0730 hours. DO at 15 meters ranged from

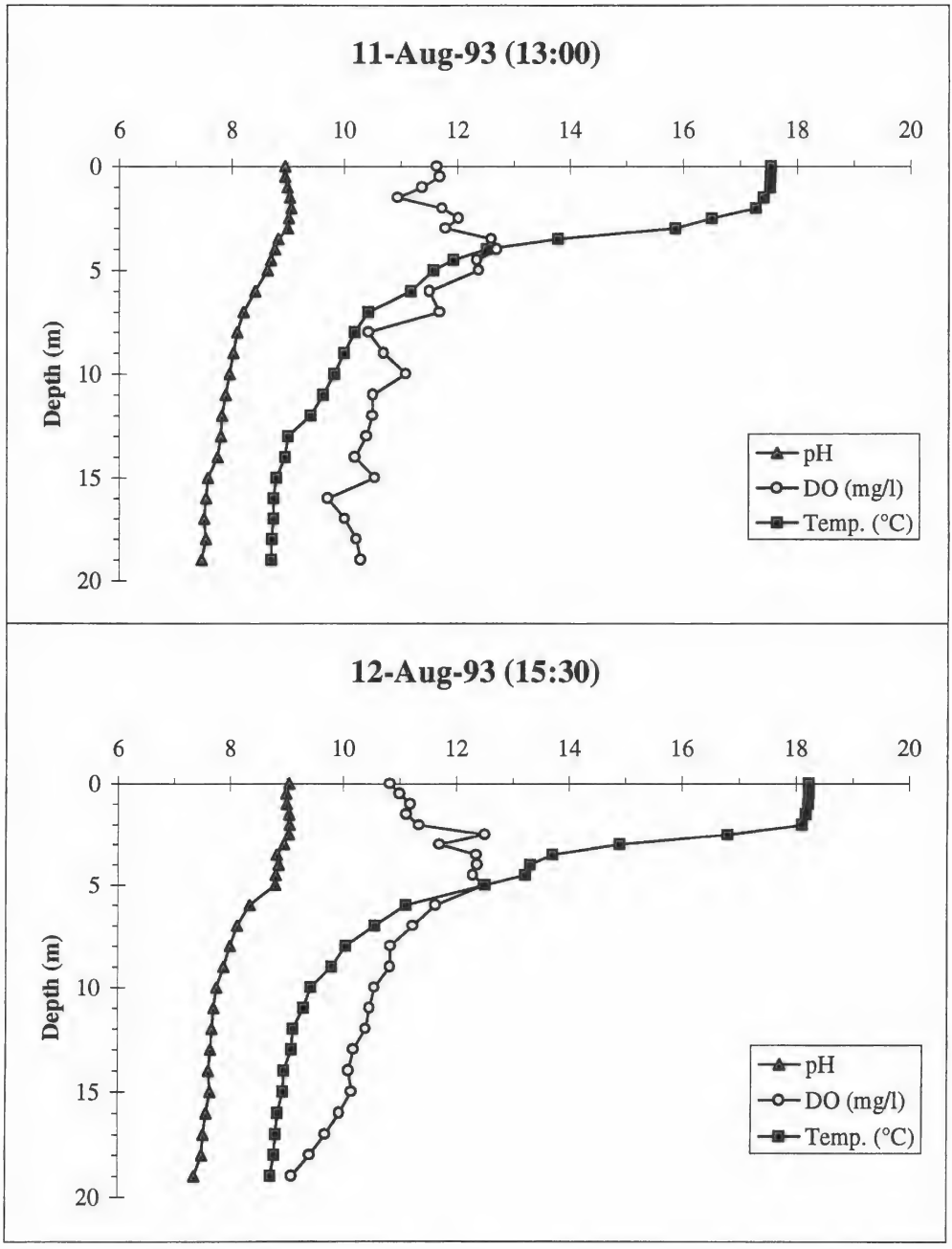

Figure 2. Vertical profiles of pH, DO (mg/L), and temperature (°C) measured in Lemolo Lake diel study, August 11 and 12, 1993.

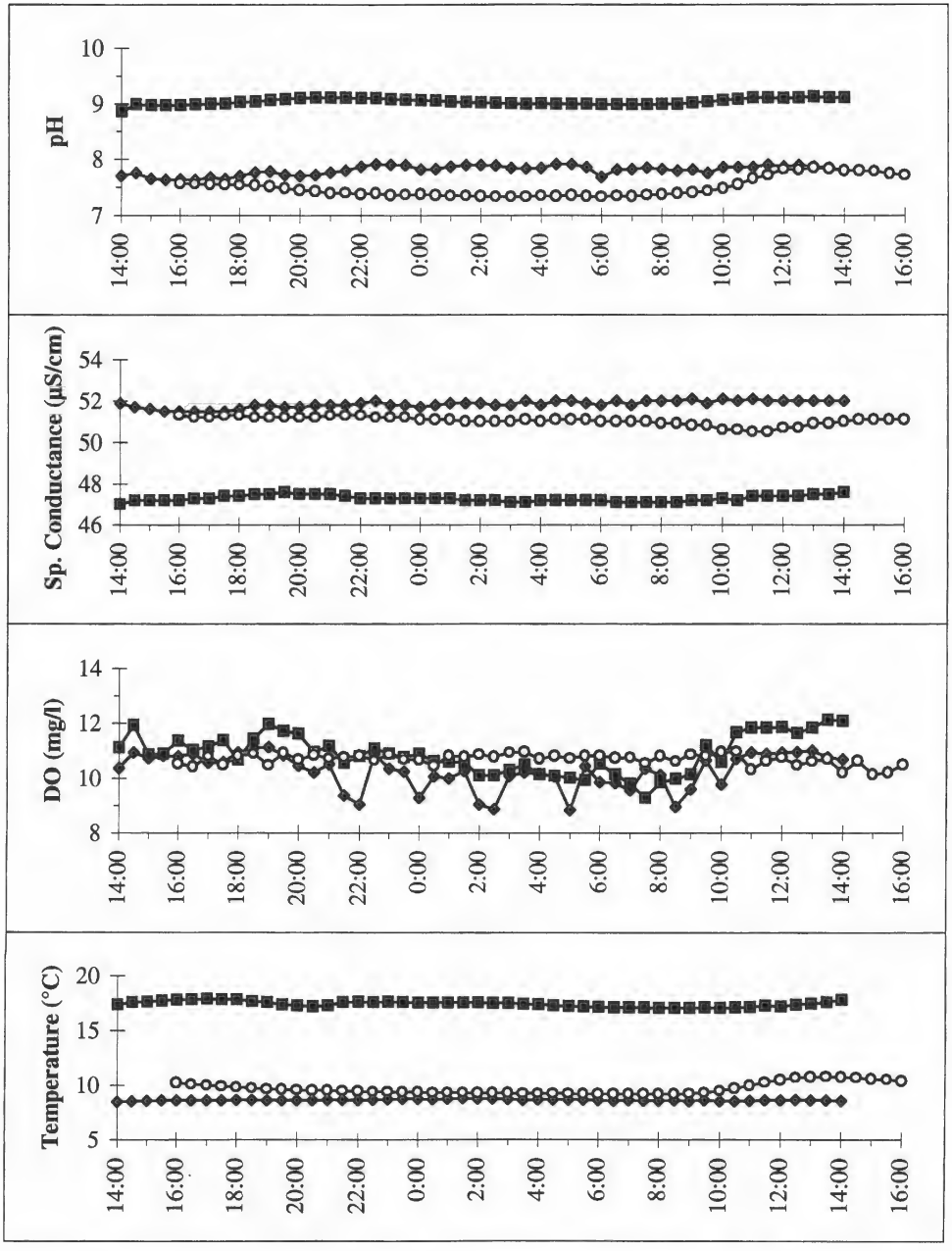

Figure 3. Results of continuous monitoring during Lemolo Lake diel study, August 11 and 12, 1993. ■ = 2 meters, ◆ = 15 meters, o = USGS gage in North Umpqua River below Lemolo Lake.

76 to 95% of saturation. At 15 meters, maximum DO concentrations occurred at 1900 on August 11; and minimum DO at 0500 on August 12.

DO concentrations in the North Umpqua River downstream of the dam were more stable than either of the reservoir depths. The minimum DO concentration measured at the USGS gage, 10.1 mg/L, was well above the minimum in the lake at 15 meters (8.8 mg/L). Average DO was 94% of saturation at the USGS gage, and 88% at 15 meters in Lemolo Lake. Re-equilibration of water released from the reservoir was therefore nearly complete at the USGS gaging station.

Active primary production in Lemolo Lake caused a markedly higher pH at a depth of two meters than at the other two monitoring locations. Average pH was 9.0 at two meters and 7.8 at 15 meters. At two meters, pH ranged from 8.9 to 9.1. pH at the USGS gage in the North Umpqua River and at 15 meters in the reservoir were similar throughout the study. Average pH at the USGS gage was 7.5, ranging from 7.3 to 7.9. Average pH at 15 meters was 7.8, and values ranged from 7.6 to 7.9.

Average values of specific conductance were consistently lower at two meters in Lemolo Lake than at the other two sites. Specific conductance at 15 meters and the USGS gage site were very similar. The overall range in specific conductance was 47 to 52 µS/cm.

Water Quality

Chlorophyll *a* concentrations were 28.4 µg/L on August 11, and 33.4 µg/L on August 12, strongly indicative of bloom conditions (Table 1). The large algal biomass elevated turbidity levels and reduced water clarity. Turbidity of 3.4 and 4.0 NTUs on 11 and 12 August, respectively, was three times the average of 1.2 NTU for surface samples collected from June 1992 through September 1994 (n=15). A Secchi depth of 2 meters on both days was less than half of the average of 5.1 meters (n=17) for the period previously described .

Total phosphorous concentrations of 36 µg/L on August 11, and 25 µg/L on August 12 were typical of surface measurements from June 1992 through September 1994 (average 40 µg/L, n=16). Ortho-phosphorus concentrations of 12 µg/L on August 11, and less than 10 µg/L on August 12 were markedly lower than the 22 µg/L average (December 1992 through September 1994, n=9).

Total Kjehldahl nitrogen (TKN, ammonia plus organic nitrogen) was 370 µg/L on August 11, and 210 µg/L on August 12. Six of 16 monthly TKN measurements from December 1992 through September 1994 were less than the 100 µg/L instrument detection limit. The average of 10 detectable readings over this period was 240 µg/L.

Inorganic nitrogen (nitrate + nitrite) was below the detection limit of 50 µg/L N on both days of the study, and in each surface sample collected on a monthly basis from April through October 1993. Detection limits were lowered to 5 µg/L in 1994; surface concentrations were less than 5 µg/L in July 1994, and 11 µg/L in September 1994.

TKN to total phosphorus (N:P) ratios on August 11 and August 12 were 10:1 and 8:1, respectively, indicative of nitrogen limitation (Welch

TABLE 1. Chlorophyll *a*, turbidity, Secchi depth, and nutrients measured in surface samples during July and September 1993, and during Lemolo Lake diel study, 11 and 12 August, 1993. Average values and ranges are from periodic monitoring; June 1992 through September 1994. LD = less than detection.

Date	Chlorophyll *a* (µg/L)	Turbidity (NTU)	Secchi Depth (m)	Total Kjeldahl N (µg/L)	NO_2+NO_3 (µg/L)	Total P (µg/L)	Ortho P (µg/L)
7-12-93	1.00	0.4	6.2	160	LD@50	24	10
8-11-93	28.4	3.4	2.0	370	LD@50	36	12
8-12-93	33.4	4.0	2.0	210	LD@50	25	LD@10
9-12-93	6.4	0.3	8.7	170	LD@50	21	LD@10
Average[1]	7.6 (n=15)	1.2 (n=15)	5.1 (n=17)	24 (n=10)	LD[2] (n=10)	40 (n=16)	22 (n=9)
Range	1-33.4	<0.1-4.2	2.0-8.7	<100-720	<5-<50	21-130	<10-50

[1]Results are from surface grab samples with levels greater than detection limits.

[2]Analyses beginning April 1993; no detectable nitrate + nitrite in 1993 (<50 µg/L) or in 1994 (<5 µg/L)

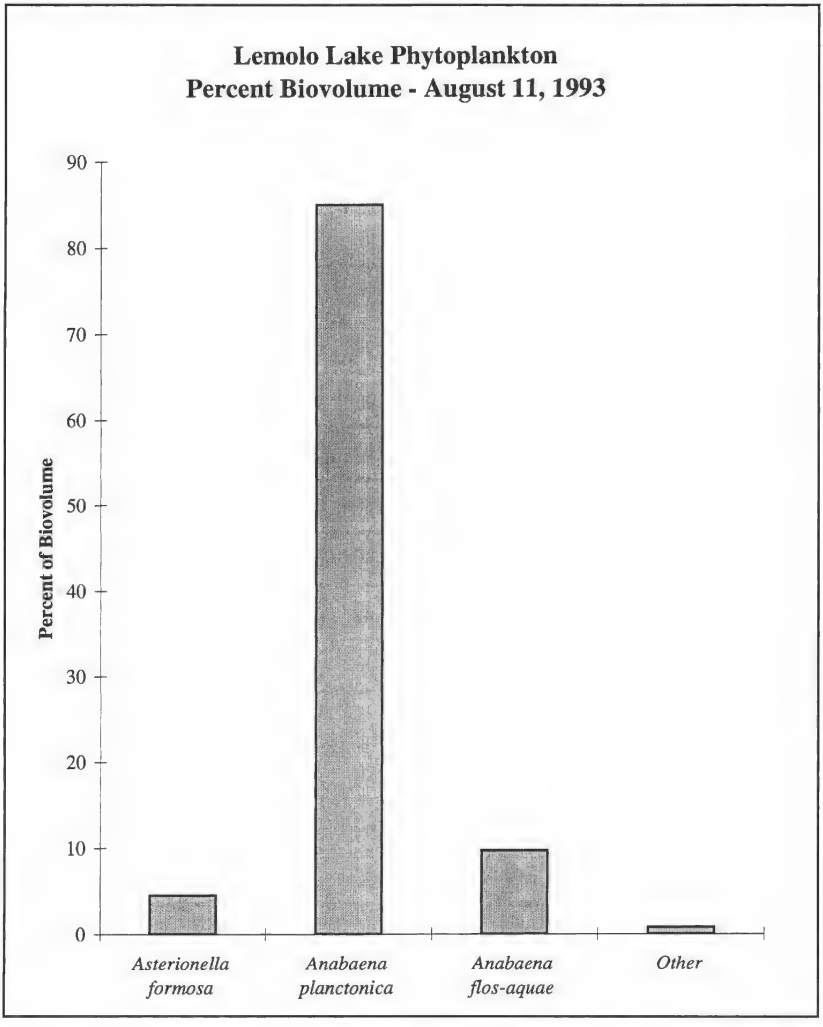

Figure 4. Lemolo Lake phytoplankton, August 11, 1993. Note: total biovolume of sample = 4,705 cu. µM/L.

1980). This ratio was used instead of soluble N:P ratios to assess nutrient limitation because nitrate + nitrite was not detected above 50 µg/L. The average N:P ratio (similarly determined) in surface samples from Lemolo Lake (1992-1994) was approximately 7:1.

Phytoplankton

Phytoplankton analyses indicate that the chlorophyll *a* concentrations were largely due to the blue-green algae *Anabaena planktonica* and *Anabaena flos-aquae*, the dominant species present in the sample (Figure 4). These species made up 95% of the phytoplankton biovolume (4,705 μm^3/L). *Anabaena* are cyanobacteria capable of fixing nitrogen, providing a competitive advantage during periods of low nitrogen availability.

In contrast to the August sample, phytoplankton samples from Lemolo Lake in spring and fall 1993 were dominated by diatoms (PacifiCorp 1995). *Stephanodiscus* sp. and *Asterionella formosa* made up over 80% of the spring and fall

samples collected from Lemolo Lake. Blue-green algae were entirely absent from the May sample, and were 5% of the biovolume in October.

Zooplankton

Total zooplankton densities were low in Lemolo Lake, however; species composition was characteristic of a mesotrophic lake with moderate amounts of organic material (pers. comm., A. Vogel, ZP Taxonomic Services, October 14, 1993; Table 2). The short retention time of Lemolo Lake (approximately 15 days) is a critical factor in limiting zooplankton densities. Reduced food quality due to the dominance of blue-green algae may also limit numbers of zooplankton.

Large cladocerans, *Daphnia galeata mendotae* and *Daphnia pulicaria*, were relatively abundant in the August sample. Their presence in moderately high numbers is indicative of low planktivory by the fish community. Other cladocerans observed included *Daphnia schloderi*, *Bosmina longirostris*, and *Chydorus sphaericus*. The majority of copepods in the sample were present as nauplii, reflective of short retention time in Lemolo Lake. Cyclopoid copepodites, *Eucyclops agilis*, and Harpacticoid copepods were also observed in the sample. Rotifers were relatively abundant and numerically dominant. *Polyarthra vulgaris* and *Asplanchna priodonta* were the most common rotifers observed.

TABLE 2. Zooplankton density (no. per m^3) in Lemolo Lake, 11 August, 1993.

Species	Density	Standard Error[1]
Cladocera		
Daphnia pulicaria	137.3	21.2
Daphnia galeata mendotae	65.4	14.6
Bosmina longirostris	16.4	7.3
Daphnia schloderi	9.8	5.7
Chydorus sphaericus	9.8	5.7
Total cladocerans	**238.7**	**27.9**
Copepoda		
Copepod nauplii	68.7	15.0
Cyclopoid copepodites	9.8	5.7
Eucyclops agilis	6.5	4.6
Harpacticoid copepods	3.3	3.3
Total copepods	**88.3**	**17**
Rotifera		
Polyarthra vulgaris	434.9	37.7
Asplanchna priodonta	415.4	36.9
Trichocerca cylindrica	163.5	23.1
Conochilus sp.	62.1	14.3
Other rotifers	58.9	NA[2]
Total rotifers	**1134.8**	**60.9**

[1]Standard error determined by: (1/sq. root of # individuals)* density

[2]Average standard error for unidentified rotifers: 5.3.

Discussion

Limnological data collected in Lemolo Lake during a period of intense primary production were indicative of eutrophic conditions. The large increase in chlorophyll *a* from July to August of 1993 (1 mg/m^3 on July 12, to 28 and 33 mg/m^3 on August 11 and 12) is indicative of the strong competitive advantage of N_2 fixing *Anabaena* in a nitrogen limited system. A large increase in chlorophyll *a* (2.7 to 11.5 mg/m^3) was also observed in Lemolo Lake from July to August of 1992 (PacifiCorp 1995). Secchi depth was markedly reduced during these periods, and daytime epilimnetic pH was near 9.0.

A distinct feature of Lemolo Lake and a key factor in production of summer algae blooms is the distinct layering of the reservoir, despite the short retention time. Slow growing cyanobacteria, large bodied *Daphnia*, and large swings in pH and DO in the surface waters are characteristic of a eutrophic lake. The warmer surface waters are trapped on top of the reservoir, and most likely have a much longer retention time than the reservoir as a whole. In contrast, the hypolimnion of Lemolo Lake is more riverine, with relatively high dissolved oxygen and little sign of impaired water quality.

The layering of the reservoir discussed above is due in large part to thermal differences between the two major tributaries to Lemolo Lake: the North Umpqua River and Lake Creek (the outflow from Diamond Lake). Lake Creek discharge during the 1993 summer low flow period (June 22 to September 21) was 0.4-0.9 m^3/s (15-30 cfs), less than 10% of the total inflow to Lemolo Lake. However, temperatures near the mouth of Lake Creek during the summer of 1993 ranged from 4-18°C (median 12°C), while North Umpqua River temperatures near the inlet to the reservoir ranged

from 4-9°C (median 6°C) (PacifiCorp 1995). Lake Creek inflows would therefore have a greater effect on the epilimnion, and may be retained longer than inflows from the North Umpqua River.

This study did not attempt to determine causal factors for the algae bloom in Lemolo Lake. However, nutrient contributions from Diamond Lake, via Lake Creek may be a contributing factor. Summer dominance of blue-green algae, seasonal algae blooms, and associated high pH have been reported in Diamond Lake, and hypolimnetic oxygen depletion occurs in both winter and summer below 10 meters (Lauer et al. 1979, Sweet 1985, Salinas 1994). Lauer et al. (1979) attributed Diamond Lake's productivity to natural nutrient loading, despite dramatic increases in lake use since the early 1920's. Recreational use of Lemolo Lake is comparatively limited, and expected to have minimal impact to water quality in the reservoir.

Growth of *Anabaena* in Lemolo and Diamond Lakes is apparently rapid, and blooms are of relatively short duration. Salinas (1994) found that chlorophyll *a* in Diamond Lake decreased from 48.7 µg/L on October 7, 1988 to 4.7 µg/L on October 21, 1988. An order of magnitude decrease in phytoplankton biovolume was observed during this period. Chlorophyll *a* in Lemolo Lake (summer of 1993) reflected extremely rapid growth from mid-July to mid-August, and a large reduction in algal biomass by mid-September.

No data were collected during the study to determine the influence of internal nutrient loading on water quality. However; hypolimnetic oxygen levels were greater than 8 mg/L, and it is unlikely that there is substantial internal loading.

The eutrophic conditions observed in the surface waters of Lemolo Lake had little effect on *in situ* variables monitored in the North Umpqua River downstream of the dam. Aeration between the dam and the USGS gage site (approximately 800 meters) increased oxygen concentration by over 1 mg/L relative to hypolimnetic values. Average oxygen concentration at the USGS gage site was 94% of saturation over the 24-hour period.

Summary

Limnological data (profiles and continuous measurement of temperature, DO, pH, and specific conductance) collected in Lemolo Lake during a period of intense primary production were indicative of eutrophic conditions. Chlorophyll *a* concentrations for samples collected August 11 and 12, 1993 were 28.4 and 33.4 µg/L, respectively; as compared to 1 µg/L in July and 6 µg/L in September. Phytoplankton biomass was dominated by the blue-green algae *Anabaena*, a nitrogen-fixing cyanobacteria. Secchi depth was markedly reduced during the study period, and epilimnetic pH remained near 9.0 during the 24 hour study.

Results of continuous monitoring at depths of 2 and 15 meters in Lemolo Lake reflected significant photosynthetic activity in the epilimnion, but minimal depletion of hypolimnetic DO (76% to 95% of saturation). Measurements of temperature, pH and specific conductance in the North Umpqua River were similar to hypolimnetic values, and in-river DO concentrations averaged 94% of saturation over the study period.

This study highlighted the existence of a surface layer in Lemolo Lake which can become highly productive during the summer months. Overall retention of the reservoir is short (15 days), but slow growing cyanobacteria and large bodied cladocerans are indicative of longer retention of Lemolo Lake surface waters. *Anabaena's* ability to remain buoyant, and to fix atmospheric nitrogen are highly adaptive to the bi-layered, nitrogen poor Lemolo Lake system.

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Processes Influencing Water Quality in a Subalpine Cascade Mountain Lake

Abstract

A study of Lake Notasha was undertaken to elucidate the major factors controlling water quality in a wilderness lake in the Oregon Cascades. The objective was to improve our understanding of ultradilute subalpine aquatic systems and thus to provide a framework for management decisions. The study focussed on understanding important lake and watershed processes by addressing variability associated with vastly different temporal scales: (1) reconstructing lake history through an analysis of the sediments, thus providing information on long-term processes; and (2) measuring components of lake hydrology and water chemistry to develop model representations of acid-base chemistry and nutrient cycling, as influenced by short-term processes.

The analysis of sediments showed that with one major exception, Lake Notasha has remained relatively unchanged for the past 6,600 years since the lake received considerable ash and tephra from the eruption of Mt. Mazama (now Crater Lake). Reconstruction of the pH and conductivity using a diatom calibration set from the Sierra Nevada indicates that the lake has been oligotrophic, dilute, and slightly acidic (pH ≈ 6.0). Approximately 3000 years ago the lake experienced a shift in dominance of diatom species, but the essential nature of the lake appears unchanged. The accumulation of sediment over the past 6,600 years has been low with a maximum average sedimentation rate of only 0.06 mm/yr.

The short-term hydrological and chemical analyses of the lake were consistent with the long-term history inferred from the sediment analyses in suggesting a highly stable environment. Nearly all base cation inputs to the lakewater can be explained on the basis of snow and rain chemistry. Over 95% of the hydrologic input to Lake Notasha occurs as precipitation on the lake surface. Most of the NH_4^+, NO_3^-, and to a lesser extent SO_4^{2-} are consumed in the lake, resulting in a net production of alkalinity. Thus, despite the extraordinarily low base cation concentrations in Lake Notasha ($C_B \approx 20$ μeq/L), alkalinity is maintained near 10 μeq/L and the lake appears resilient to modest additional atmospheric inputs of SO_4^{2-} or NO_3^-. Lake Notasha appears to be largely hydrologically isolated from its terrestrial catchment, a feature which promotes biological and chemical stability of the lake.

Introduction

An inevitable consequence of continued population growth and industrial expansion is increased conflict between human demands on natural resources and the maintenance of pristine lakes and streams. Although progress has been made in affording protection for many alpine and subalpine lakes through the passage of the Wilderness Act (PL 88-577, 1964), the designation of wilderness does not guarantee that degradation will not occur. The water quality of lakes, even in wilderness areas, may be threatened as a consequence of air pollution, recreation-related activities, or mineral exploration. Because of the fragile state of some of the pristine wilderness resources, it is possible that management activities which may be appropriate in low elevation settings cause unforeseen changes at high elevation sites.

Lake Notasha contains concentrations of dissolved minerals comparable to that in precipitation and is one of the most dilute lakes reported (Eilers et al. 1990). The lake is located in the Sky Lakes Wilderness in an area frequented by backpackers and horsepackers. High usage has resulted in damage to vegetation bordering Lake Notasha and other lakes in the Sky Lakes Wilderness. The Winema National Forest has cordoned off some small areas and replanted the overused sites. The lake originally lacked a fish population, but has been stocked with salmonids by the Oregon Department of Fish and Wildlife since at least 1947.

Lake Notasha was considered an appropriate wilderness study lake because of the availability of previously collected data (Eilers et al. 1987, 1990), its small size, relatively easy access, high recreational use, and high water quality judged to be sensitive to anthropogenic inputs of acids

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or nutrients. The specific objectives of this study were to: (1) evaluate long-term changes in Lake Notasha through paleolimnological analyses of the lake sediments; and (2) measure short-term changes in lake chemistry and hydrology that might provide insight into the major watershed processes controlling lakewater quality.

Site Description

Lake Notasha is a small, subalpine lake located near the crest of the southern Oregon Cascades in the Sky Lakes Wilderness, Winema National Forest. The lake is located in Klamath County and is proximate to two well known lakes—Crater Lake which is about 50 km to the north and Upper Klamath Lake, 15 km to the southeast. The lake is located 4 km from a major trailhead, the Cold Spring Camp near the Pacific Crest Trail. Lake Notasha is one of about 200 glacial ice-contact lakes and ponds formed in the area during the retreat of the most recent glaciation (Smith 1983, Smith and Benham 1984). Lake Notasha is located at the headwaters of the Rock Creek drainage, but the lake itself has no permanent surface inlets or outlets, and the immediate topographic watershed is only about 5 ha. The lake has a maximum surface area of 2.7 ha and has a maximum depth up to 10.6 m. The mean depth of the lake is about 5 m (Figure 1). The lake was previously described by Eilers et al. (1990, 1994).

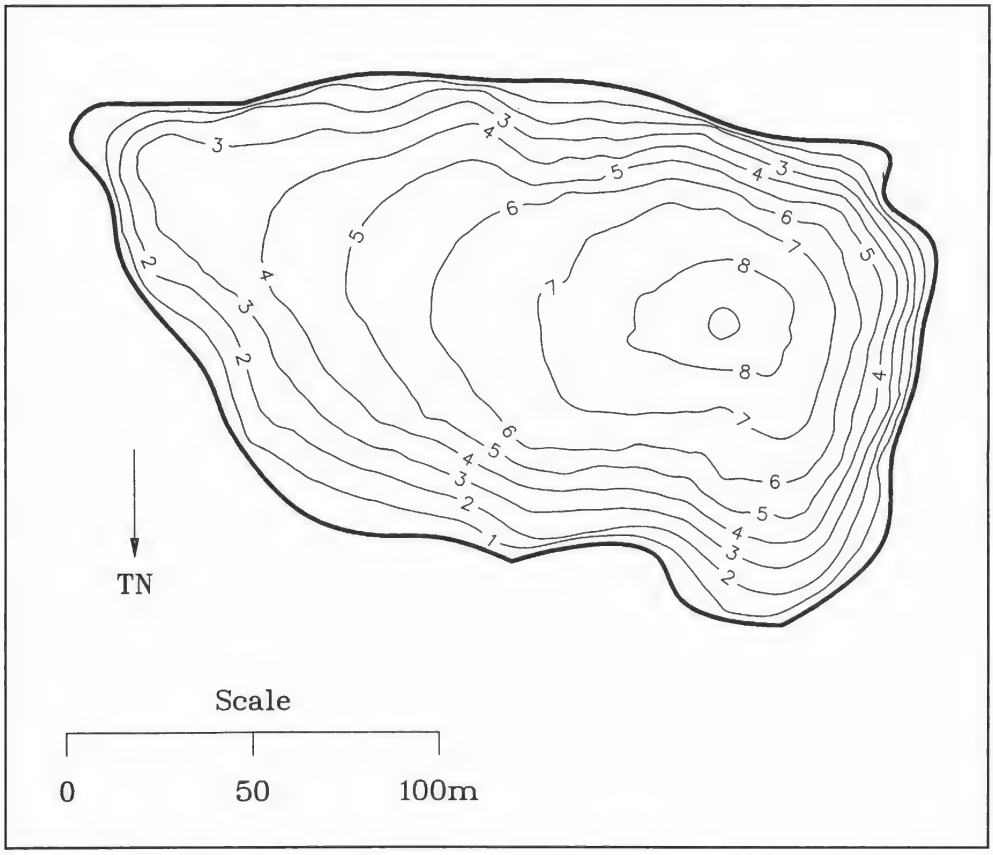

Figure 1. Bathymetry of Lake Notasha (in meters) measured on October 16, 1993 using methodology of Gubala et al. (1994). Staff gage was at 0.68 m above arbitrary datum. Maximum depth at the time of the lake mapping was 9.5m, whereas depths up to 10.6 m were recorded during the study.

Methods

Surface water samples were collected from the center of the lake by lowering a Van Dorn sampler 0.5 m under the surface, or in some cases, by submerging a 1-L Nalge bottle to 0.5 m depth by hand. Water samples were chilled using gel-packs, snow, or insulated containers and were transported immediately to Cold Spring Camp. Water samples were then kept on ice prior to and during transit via overnight courier to the analytical laboratories.

The primary analytical laboratory used for the study was the Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, operated by the USDA-Forest Service. Samples were analyzed immediately upon receipt for non-conservative constituents and preserved for subsequent analyses of the remaining constituents. Maximum holding times were those recommended by Standard Methods (APHA 1989). Analytical methods were similar to those used in EPA's Western Lake Survey (Landers et al. 1987) where base cations (Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}) were analyzed using a Thermo-Jarrell Ash ICP-AE (inductively coupled plasma-atomic emission). Acid anions (SO_4^{2-}, NO_3^{-}, Cl^{-}) were analyzed using a Dionex ion chromatograph and the concentrations were computed by integrating the area under the curves. pH and alkalinity were measured using the Acid Rain Analysis System (ARAS) by Radiometer. The system is programmed to automatically measure pH and compute acid neutralizing capacity using a Gran function. Conductivity was measured in the laboratory and also was calculated by summing the equivalent conductances of measured ions. The laboratory QA/QC program is described by O'Deen et al. (1991).

Sediment was collected by lowering a 10-cm diameter piston corer supplemented with an additional 110 kg of weights. On all three attempts, the maximum length of sediment extracted from the lake was about 40 cm. The sediments collected from the third core were taken to shore and extruded in increments of 0.25 cm in the upper sediments and 1 cm deeper in the core.

Sediment organic matter was estimated by weight loss on ignition (Dean 1974). Sediment subsamples from selected depths (18 samples) were cleaned using standard acid digestion techniques for diatom analysis (Dixit 1986). Diatom taxonomy followed the designations in Camburn et al. (1984-1986).

Although no diatom calibration set currently exists for the Oregon Cascades, a calibration set for mountain lakes in the Sierra Nevada (Whiting et al. 1989) was employed in addition to the qualitative analysis. Use of the Sierra Nevada (SNEV) data set for Lake Notasha must be used with caution, principally because of the lack of analogues of some important downcore diatoms (e.g., *Pinnularia brebissonii* and *Cymbella* cf. *triangulum*) in surface sediments of SNEV lakes. Also, Lake Notasha, although similar to the high mountain low conductivity lakes sampled in the Sierra Nevada, is close to the acidic end of the pH gradient and is at the end of the conductivity gradient of these lakes. Using partial and constrained canonical correspondence analyses (ter Braak 1986) along with forward selection and Monte Carlo permutation tests, we can estimate the variance in the diatom surface sediment communities of the 45-lake SNEV calibration set that can be explained by environmental parameters and select those appropriate for paleoecological analyses. We used CANOCO version 3.21 (ter Braak 1990) for all ordinations.

These tests indicated that the six significant variables (calcium, conductivity, nitrate, latitude, pH, and watershed area) can explain 20.7% of the variance in diatom communities. Of these, calcium, pH, and conductivity are all slightly correlated and represent various aspects of the acid/base chemistries of these lakes. pH (3.6%) and conductivity (3.9%) independently make a significant contribution (Monte Carlo test, 999 unrestricted permutations at $P < 0.05$) to the diatom variance.

Reconstructions of past pH in Lake Notasha were performed using WACALIB (Birks et al. 1990). This program constructs a diatom transfer function using weighted averaging regression. The diatom transfer function for pH for the SNEV calibration set has an apparent R^2 of 0.81 and a RMSE of 0.36, and conductivity (after $\log_{10}$ transformation) has an apparent R^2 of 0.74 and a RMSE of 0.22. However, the predictive ability of the function is probably better assessed using the jackknifed root mean square error of the prediction or RMSEP (ter Braak and Juggins 1993). Using the program CALIBRATE (Juggins and ter Braak 1992), we calculate the RMSEP of pH to be 0.4708 and conductivity ($\log_{10}$) to be 0.302.

In order to date the core increments, 13 sediment subsamples from selected depths were

analyzed for ^{210}Pb. Staff at the Chalk River Nuclear Laboratory, Chalk River, Ontario, analyzed the subsamples using a microwave digestion technique and measured ^{210}Po activity using alpha spectroscopy. The recent dates were computed using the CRS (Constant Rate of Supply) model of Appleby and Oldfield (1978). Dates greater than 150 years were estimated using a regression relationship between ^{210}Pb dates and accumulated sediment depths ($r^2 = 0.99$).

A 1.0 m lake stage gage was installed at the lake by attaching it to a board and anchoring it at the base of a boulder. Remote data collection devices were installed to record lake temperature (thermistor) and air temperature (thermistor) at 15-minute intervals, and precipitation amount (tipping bucket gage). Data were stored in a Campbell Scientific data logger and downloaded onto a laptop computer during periodic visits to the lake. Power was provided by a deep-cycle marine battery buried on-site.

Results

Paleolimnology

Percent water content and loss-on-ignition (LOI) of sediment samples provide some indication if sediment conditions have remained uniform within a given lake. The water content remained similar in sediments deposited below the 12 cm core depth (pre-720 YBP), but a distinct decline in both water content and LOI occurred at the 9 cm depth (390 YBP; Figure 2).

The age of the bottom sediment, based on the regressed ^{210}Pb activity, was about 6,600 YBP. The average sediment accumulation rate for the compacted portion of the core (12-39 cm) was about 0.05 mm/yr, only slightly less than the overall rate of accumulation (0.06 mm/yr). The extrapolated date for the bottom sediment in Lake Notasha corresponds closely with the eruption and collapse of Mount Mazama in southern Oregon about 6,850 YBP (Bacon 1983, Abella 1988). The

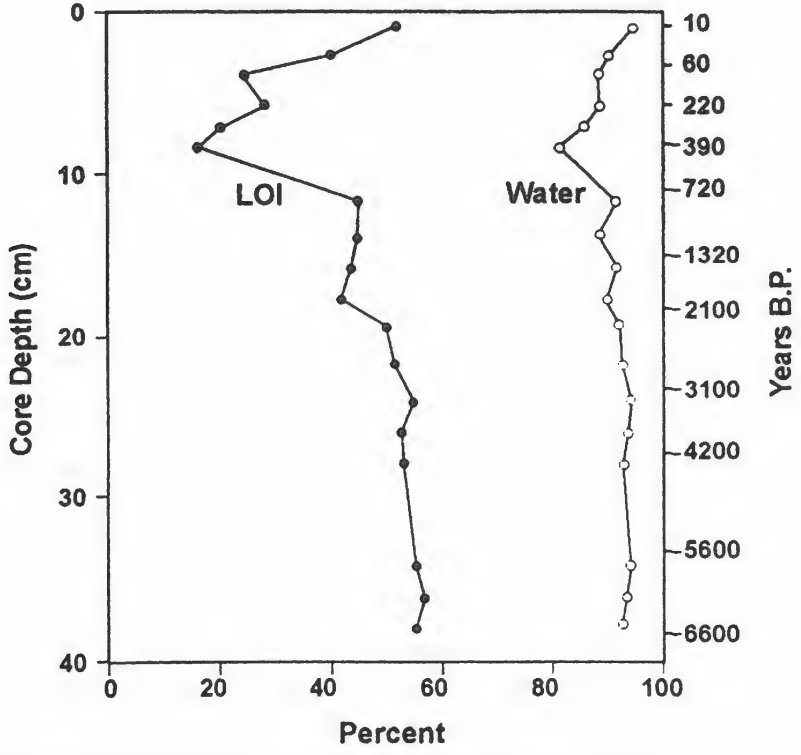

Figure 2. Water content (%) and loss-on-ignition (%) for the sediment of Lake Notasha.

extrapolated age of the base of the core at ~6,600 YBP is also consistent with the physical evidence in the field: (1) the appearance of a light ash-like material at the base of the core, and (2) the repeated resistance to core penetration of the lake sediments at a depth of about 40 cm.

Sedimentary diatoms were identified and counted from 18 sediment depths. The diatoms were well preserved throughout the core. A total of 82 diatom taxa were identified (Eilers et al. 1994), the most common of which are presented in Figure 3. The diatom population in the lower portion of the core (pre-3,600 YBP) is dominated by *Pinnularia brebissonii, Melosira distans* v. *nivalis, Frustulia rhomboides* v. *saxonica*, and *Cymbella hebridica. Pinnularia brebissonii* prefers cool water of low mineral content (Patrick and Reimer 1966). From the bottom of the core to 26 cm, *P. brebissonii* declined in abundance although it remains the dominant taxon.

The results of the diatom-inferred changes in pH and conductivity derived from the SNEV calibration set are presented in Figure 4. Despite some substantial shifts in the diatom composition in the sediments, the magnitude of the changes in inferred pH and conductivity are relatively small. The inferred pH change over the entire period of record is less than 0.3 units and inferred conductivity declined only 2 μS.

Although *P. brebissonii* is a major taxon in Lake Notasha, this diatom plays no role in the inferred changes because it is absent from the SNEV calibration set and is poorly represented in other large calibration sets of the United States. Consequently, the major driving factor in the inferred pH profile is probably the increase in a suite of low-pH taxa, particularly *Melosira distans v. nivalis*, which has the lowest abundance weighted mean pH of any of the important SNEV diatom taxa (5.91). Thus, in terms of diatom-inferred pH, the period from 6,600-4,900 YBP is static with pH between 6.3 and 6.4. pH declines to 6.15 by 3,600 YBP in response to the floristic changes.

The diatom assemblage showed a distinct shift between 2,600 YBP and 3,600 YBP; the percent abundance of *Navicula tenuicephala* and *Pinnularia braunii* v. *amphicephala* increased, whereas *P. brebissonii, M. distans* v. *nivalis, F. rhomboides* v. *saxonica*, and *C.hebridica* declined in abundance. *Navicula tenuicephala* is generally regarded as an acidobiontic diatom with an abundance weighted mean pH of 4.9 reported for the lakes in the Adirondack region of New York (Dixit et al. 1993). However, in the Sierra Nevada, this taxon's mean pH is 6.31 (still amongst the most acidic diatoms in the SNEV) and its abundance weighted mean conductivity is 3.6 μS the lowest of any diatom in the SNEV calibration set. Furthermore, the sharp decline in the representation of *M. distans v. nivalis* is matched by an increase in the abundance of *P. braunii v. amphicephala* (6.1) and *Achnanthes marginulata* (6.1) that are the second and third most acidophilic diatoms in the SNEV. Therefore, the abundance weighted mean pH does not respond to this large floristic change, but the inferred conductivity registers its largest decline and lowest level in the core.

The diatom taxa in this upper section have similar ecological tolerances to those taxa in the Sierra Nevada and there is little response in the inferred pH and conductivity profiles to the slight floristic fluctuations seen between 2,600 and 60 YBP. There are floristic changes in the last century, principally a decrease in the representation of *P. braunii v. amphicephala* and *A. marginulata*, and a rise in *N. tenuicephala*. During this time it appears that pH may be showing a small increase. The surface sediment inferred pH and conductivity are very close to the measured values (6.21 versus 6.03, 3.3 versus 2.9 μS).

Lake Chemistry

The chemistry of Lake Notasha measured during the period of 1992-1993 shows a very dilute system that exhibits small seasonal variation in major ion chemistry (Figure 5). Similar to other subalpine and alpine lakes, Lake Notasha contained minimum base cation concentrations in July, 1993, shortly after snowmelt. The principal base cations (Ca^{2+}, Mg^{2+}, Na^{+}) increased through the summer and into fall as solutes were concentrated due to evaporation. Sulfate and chloride also increased slightly throughout the late summer and fall, which again is consistent with evapoconcentration. pH reached a minimum under the ice, presumably from CO_2 saturation (cf Kratz et al. 1987), and increased through the summer possibly in response to increased primary productivity. Acid neutralizing capacity (ANC) reached a minimum in October 1992, but increased through September 1993, declining slightly in the fall. Silica showed a major increase from November to March in what

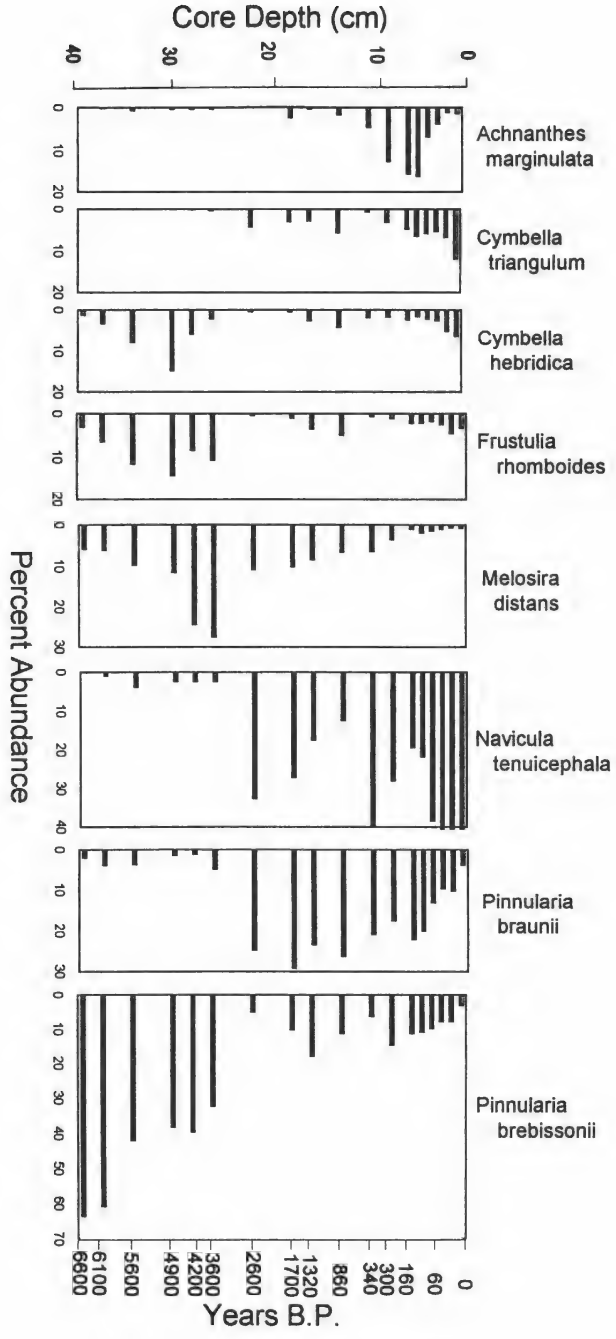

Figure 3. Relative abundances of common diatom taxa in the sediment core from Lake Notasha.

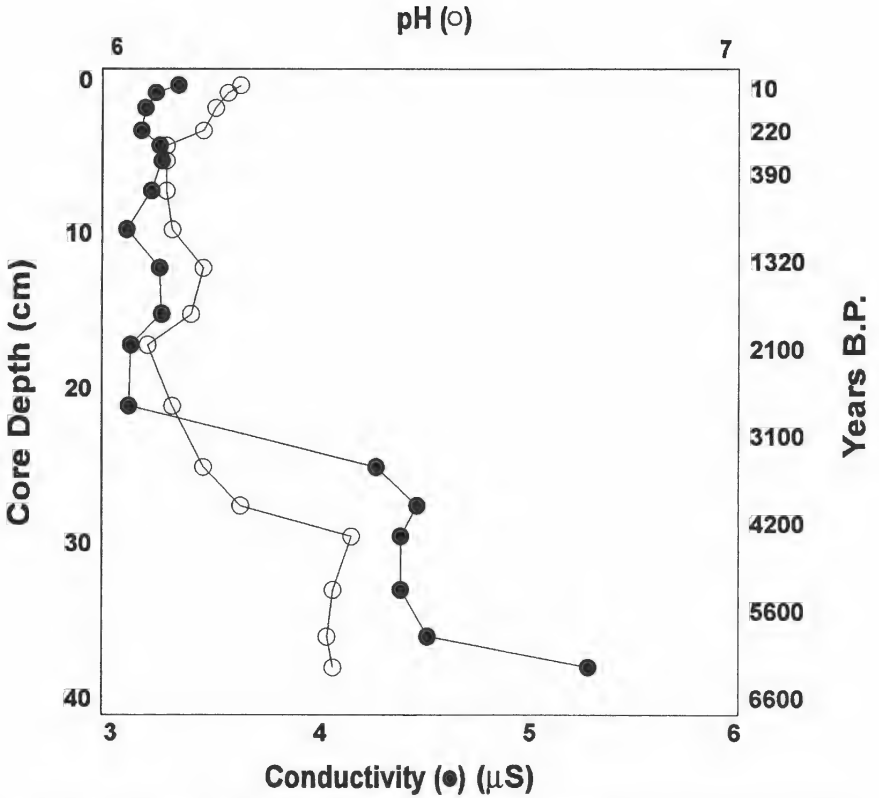

Figure 4. Diatom-inferred changes in pH and conductivity (μS) for Lake Notasha based on a calibration set of Sierra Nevada lakes.

appears to be dissolution of silicate minerals from sedimentary diatoms (note there was no corresponding increase in base cations which would indicate a watershed source of silica). Silica concentrations declined steadily through the summer, as inputs declined and biological uptake incorporated what little silica was available. Nitrite and ammonium concentrations were low but exhibited some measurable variability. Nitrate concentrations increased in the fall through winter and became undetectable in the summer as NO_3^- was assimilated for primary productivity. Ammonium decreased from fall through spring, and like nitrate was not measurable in the summer. However, NH_4^+ became detectable once again in the fall whereas NO_3^- remained undetectable.

Major ion chemistry for Lake Notasha and other selected nearby lakes, streams, and precipitation samples collected during the study are summarized in Table 1. The results show that adjacent South Heavenly Lake is chemically indistinguishable from Lake Notasha. A simple mixing model of snow (allowing for evapoconcentration in the summer) and groundwater (as reflected in chemistry from Cold Spring) indicates that the chemistry of these two lakes can be explained by over 95% of the input volume from snowfall on the lakes with the balance as groundwater and snowmelt inputs from the watershed. This may overestimate watershed inputs because the calculation does not account for rainfall and dryfall inputs during the summer which would be expected to have a greater proportion of base cations than winter snowfall.

Discussion

The diatom remains in the sediment indicate that the acid-base chemistry of Lake Notasha has been

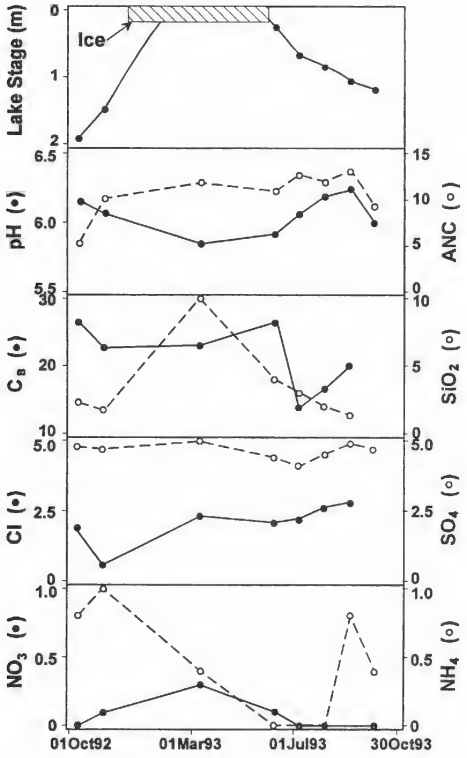

Figure 5. Changes in the major ion chemistry of surface waters in Lake Notasha during WY1993. Lake stage is in meters above an arbitrary datum. All ions are presented in microequivalents per liter; silica is in micromoles.

remarkably stable over 6,600 years. The largest floristic change recorded in the sediments between 3,600 and 2,600 YBP coincides with results of palynological studies indicating that the climate in the Northwest was cooler and moister during this period (Mack et al. 1978 a,b). All inferred changes in lake chemistry are so small as to be statistically unimportant. Despite the cautions regarding the use of the Sierra Nevada diatom calibration set for Lake Notasha, the reconstructions of the lake chemistry accurately reflect current pH and conductivity. The Sierra Nevada calibration lakes are similar to Lake Notasha in many respects: remote, western mountain lakes that are extremely dilute, with pH values typically between 6 and 7. Despite the lack of an analogue in the Sierra Nevada for *P. brebissonii*, an average of 62% of the diatoms in the Notasha core had representative analogues in the SNEV calibration set. The flora of Lake Notasha was represented by a combination of those diatoms that were among those representing the most acidic and most dilute lakes in the SNEV calibration set. We therefore have confidence in the diatom-inferred reconstructions performed on Lake Notasha.

On an annual basis, fluctuations in the chemistry of Lake Notasha were small, with variations of only several microequivalents per liter for all ions combined. Nutrient concentrations were low (TP < 1 µg/L, TIN < 13 µg/L, Eilers et al. 1987) and often undetectable. Silica concentrations exhibited some seasonality, presumably associated with inputs from the watershed in the spring followed by declines in the summer from biological uptake.

Despite its remarkably dilute nature, Lake Notasha is not unique in the Sky Lakes Wilderness. The chemistry of nearby South Heavenly Twin Lake (Table 1, Figure 6) is virtually indistinguishable from Lake Notasha. However, several other lakes in the immediate area have higher concentrations of base cations illustrating the importance of local hydrologic flowpaths in influencing the chemistry of these systems. Using Ca^{2+} as a semi-conservative tracer to represent watershed inputs (cf. Stauffer 1985), it is evident that Lake Notasha and South Heavenly Twin Lake are dilute by virtue of their position as headwater lakes in the Rock Creek watershed. Lakes down-gradient of these two lakes apparently receive varying percentages of groundwater input depending on the hydraulic gradient and mixing of various source waters. Lake Elizabeth likely has the highest percentage of groundwater inputs because of the considerable gradient downhill from Lake Notasha (Figure 6) causing a relatively high percentage of groundwater to pass through the lower elevation lake. Although North Heavenly Twin Lake is the most down-gradient lake in the group, it has intermediate concentrations of Ca^{2+} because of the mix of dilute waters from precipitation on its large surface area and input from more concentrated source waters up-gradient.

The relative position of the lakes in the topographic sequence not only has a major influence on the chemistry of the lakes, but also influences the hydraulic residence time of the individual systems. Lake Notasha has an estimated hydraulic residence time of 5 yrs, compared to values about

TABLE 1. Mean water chemistry of lakes, streams, and precipitation measured on the Lake Notasha project (1990-1993) in the Sky Lakes Wilderness. For lakes with more than four observations, the standard deviation is indicated in parentheses. For sites with single observations, the date of sample collection is shown.

	Number of Observations /Date	pH	Alkalinity (μeq/L)	Conductivity (μS)	SiO_2 mg/L	Ca^{2+} (μeq/L)	Mg^{2+} (μeq/L)	Na^{+} (μeq/L)	K^{+} (μeq/L)	NH_4^{+} (μeq/L)	NO_3^{-} (μeq/L)	SO_4^{2-} (μeq/L)	Cl^{-} (μeq/L)
Lake													
Notasha	12	6.03 (0.12)	11 (2.8)	2.9 (0.3)	0.2 (0.17)	6.8 (2.5)	7.3 (1.7)	4.4 (1.8)	1.5 (0.4)	<0.7 —	<0.2 —	2.2 (0.7)	4.5 (0.4)
S. Heavenly Twin	5	5.98 (0.10)	11 (2.2)	3.0 (0.3)	0.4 (0.23)	6.5 (3.5)	5.6 (1.6)	7.9 (2.8)	2.9 (0.5)	<0.2 —	<1.6 —	2.6 (0.7)	4.9 (0.4)
Deer	2	6.14	22	5.4	0.5	12	8	9	5	1	ND	2	4.6
Florence	7/24/93	6.08	26	6[f]	0.3	9.4	8.3	12	1.4	1.6	ND	2.8	7.4
N. Heavenly Twin	3	6.71	63	6.6	3.4	27	12	24	1.8	1.2	ND	1.2	5.1
Liza	2	6.71	82	7.6	3.5	39	17	27	2.6	0.6	ND	1.2	5.4
Isherwood	3	6.79	89	8.2	4.3	45	17	29	2.7	0.6	ND	<0.8	5.4
Elizabeth	2	6.28	131	12.2	5.5	86	28	34	3	1	ND	1	5.8
Streams/Springs													
Cold Spring	3/14/93	6.81	337	32.0	15.0	182	147	74	4.1	ND	ND	2.4	6.0
Rock Creek	7/24/93	7.50	475	41.6	19.2	246	116	93	7.7	ND	ND	1.6	6.4
Snowmelt/runoff	6/19/93	6.72	82	8.1	4.8	56	19	23	2.0	ND	ND	1.2	5.2
Precipitation													
Snow Pit	3/13/93	5.36	0.3	3.3	0.03	4.2	1.1	3.2	1.2	<0.7	2.8	2.7	3.9

ND = not detected
f = field

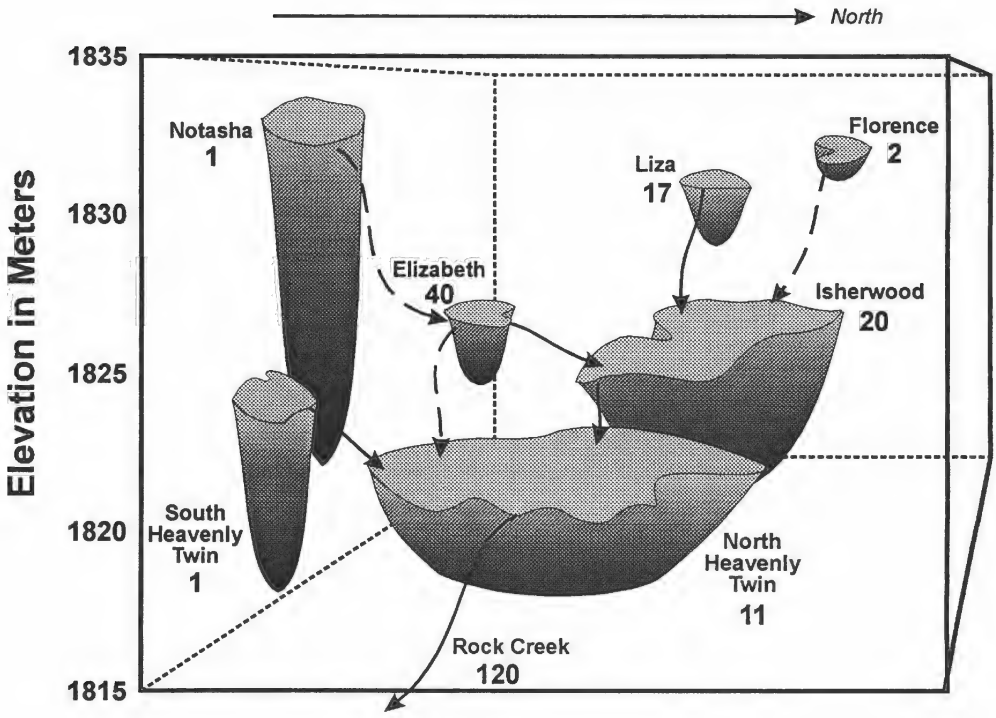

Figure 6. Relative topographic position of Lake Notasha and other adjacent lakes in the Sky Lakes Wilderness. The numbers represent the lake concentrations of calcium (μmole/L) after subtracting atmospheric contributions. Surface water flow paths are shown as solid lines; inferred groundwater contributions are shown as dashed lines. The concentration in Rock Creek is based on a sample collected about 10 km downstream from the outlet from North Heavenly Twin Lake. Lake depths are approximate.

one order of magnitude less for systems such as Lake Elizabeth. The long hydraulic residence time in Lake Notasha which acts to increase its sensitivity to anthropogenic nutrient inputs, deceases its sensitivity to acidification from atmospheric inputs of S and N. Inorganic nitrogen deposition is almost completely assimilated by the biota and about one-third of the annual SO_4^{2-} load is reduced in the lake. Assuming sulfate reduction rates remained constant, SO_4^{2-} deposition would need to increase approximately four-fold to exhaust the current acid neutralizing capacity in the lake.

The slight trend during this century towards less dilute, higher pH waters in Lake Notasha, as indicated by the sedimentary diatoms, raises questions regarding possible mechanisms associated with such a change. A climatic shift towards wetter conditions would be consistent with increased input of base cations from the watershed due to an increase in groundwater/surface water inputs. For example, headwater seepage lakes in Wisconsin decreased in base cation concentrations during a prolonged drought in response to reduced groundwater inputs (Webster et al. 1996). However, we are unaware of climatic data for the Pacific Northwest that would indicate elevated precipitation in the 20th century. Alternate explanations for the apparent trend in Lake Notasha include increased input of base cations from atmospheric deposition, increased watershed inputs caused by recent recreational activities, and changes in lake chemistry caused by fish stocking into a formerly fishless lake. An increase in atmospheric base cation deposition to Lake Notasha during this century is possible given the increasing human land use activity in the western Cascades. It is also conceivable that recreational activities along the lakeshore or fish stocking have altered the nutrient concentrations in Lake Notasha, thus increasing the lake pH. The recent changes in lake

chemistry inferred using diatom reconstructions are small and within the range of historical values. Nevertheless, lakes such as Notasha are so dilute that relatively small changes in atmopsheric and watershed inputs may cause unforeseen changes in the receiving waters.

In summary, the paleolimnologic evidence shows that Lake Notasha exhibited a modest change in diatom taxa between 3,600 and 2,600 YBP, possibly caused by a change in climate. A trend in this century towards higher pH waters is consistent with human activities in the wilderness, although the magnitude of these apparent changes are not statistically significant. Annual variations in lake chemistry were muted, with the most pronounced changes associated with biologically-mediated fluctuations in pH and silica. Lake Notasha is a remarkably dilute lake because of its landscape position in glaciated, volcanic terrain. The high hydraulic conductivity of the area promotes rapid infiltration and deep recharge of the aquifer. The small watershed contributions of groundwater that reach the lake are not highly concentrated because of the siliceous soils and bedrock weathering and short water flowpaths. The results indicate that management of dilute lakes in these settings is strongly related to maintaining the hydrologic integrity of these systems. Factors such as trail construction or compaction of the thin soils which would promote greater surface runoff would increase watershed contributions to lakes such as Notasha.

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